Echino.

Studies in Edrioasteroidea
I–IX

By F. A. BATHER

Mr. Austin Hobart Clark
with kind regards
F. A. B.

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STUDIES IN EDRIOASTEROIDEA

I–IX

BY

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October, 1915

CONTENTS.

N.B.—The numbers in square brackets are those attached to the papers in the privately issued List of my Scientific Writings.

PREFACE.

When, seventeen years ago, the first of these Studies was published in the *Geological Magazine*, the material for most of the succeeding Studies had already been accumulated and, to a large extent, described and figured. It was therefore no idle fancy that led me to anticipate the early publication of the series and caused me on that account to postpone the reprinting and distribution of separate copies. Unfortunately those plans were upset by an unexpected increase of official duties and other pressing work, so that plates already prepared in 1900 did not see the light till 1914. The Studies already published might indeed have been distributed in separate form had not all their plates been lost while in store and had not the cost of a fresh production appeared disproportionate. Lapse of time, however, has convinced me that those Studies ought to be reprinted. So many who in recent years have written about Edrioasteroidea seem to have written in ignorance of the facts therein made known, and it cannot be denied that those facts ar eof extreme interest and importance for the morphology and classification of the Echinoderma. It will be recognised that it is not for me to charge my colleagues with ignoring my own writings when I have omitted the usual courtesy of supplying them with copies. However much one is tempted to censure avoidable ignorance, one must realise the difficulties which the present unorganised condition of the scientific world places in the way of those who wish to read no less than of those who wish to be read.

So here are the Author's Copies at last. Or let us dignify them by the name of 'Author's Edition'; for, though reprinted without textual change and with the original pagination of the *Geological Magazine*, they are supplemented by this Preface and by an Index, and the Editor has most kindly allowed me to have them technically republished.

There is one change, duly noted in the *Geological Magazine* for October, 1915 (p. 478). The numbers of the rays in the Text-figure on p. 260 of the 1915 volume were inserted in the wrong order (contra-solar instead of solar), and that has been set right in this edition.

In preparing these papers, one of the most difficult tasks, as also one of the most important, was the attribution of each specimen to its precise horizon. On this matter it is possible to add a few details.

In reference to *Edrioaster buchianus* (Study II), it had escaped me that in 1885 T. Ruddy (Proc. Chester Soc. nat. Sci., III, p. 123) had written thus: "*Agelacrinus Buchianus* (Forbes), *Protaster Salteri* (Forbes), and one or two other species seen in other collections from this neighbourhood, have been found in Zones 8 and 9," that is to say in the zones which Ruddy called those of "*Strophomena expansa*" and "*Orthis alternata*", just above the "Little Ash" of the Geological Survey memoirs, at the base of the Bala series.

The horizon of *Steganoblastus* (Study V) was left doubtful. Mr. Walter Billings, however, tells me that the beds at Division Street, Ottawa, in which the specimens were found, occupy the upper 20 feet of the Trenton Limestone, as there exposed, and yielded also examples of *Archaeocrinus desideratus*, *Hybocrinus conicus*, and *Carabocrinus* sp. At 20 feet from the summit *Cyclocystoides* and *Amygdalocystis* were found. I infer that *Steganoblastus* may have

come from Dr. P. E. Raymond's Horizon 5 (see Study IV, 1914, p. 117).

I have just taken the opportunity of visiting Coalbrookdale with my friend the Rev. W. M. D. La Touche. Our object was to find further specimens of *Pyrgocystis ansticei*. In this we were not successful, owing no doubt to the growth of vegetation since the original specimens were collected. We were able, however, to identify the "Loam hole" (Study VI, 1915, p. 51), and to see that the beds of Wenlock Shale formerly exposed there must be in the lower part of that formation.

Of the Studies that in happier days may follow these, several are partly prepared and one, on *Stromatocystis*, has for several months been ready for the printer, but its illustration awaits a time when funds can be released from the needs now more vital. The present series brings the subject to a point where its bearings on general echinoderm morphology can be appreciated, and it is my hope that those who till even wider fields of biology may find here some facts and suggestions of interest to their own speculations.

These Studies owe much to friends and colleagues in many countries, but there is one who, though we have never met, has been so constant and ready in his help and encouragement that I must give myself the pleasure of mentioning his name here—Mr. Walter R. Billings of Ottawa.

F. A. BATHER.

KENSINGTON, *24 Sept., 1915.*
H.Q.—V.A.D. London/31,
Brit. Red Cross Soc.

STUDIES IN EDRIOASTEROIDEA.

By F. A. Bather, M.A., F.G.S.

I. *Dinocystis Barroisi*, n. g. et sp., Psammites du Condroz.

[Geol. Mag., n.s., Dec. IV, Vol. V, pp. 543–548, Pl. XXI ; Dec., 1898.]

Horizon and Locality.

On April 30th, 1897, the Trustees of the British Museum purchased from Dr. F. Krantz, of Bonn, seven specimens labelled "*Agelacrinus*, n.sp., Unter Devon, Condroz, Frankreich." But the Condroz is a district in Belgium, south of Namur and Liége, between the rivers Meuse and Ourthe; the species do not belong to *Agelacrinus* or any known genus; and the matrix clearly is that of the well-known "Psammites du Condroz," which are Upper, not Lower, Devonian. The species, however, is new, and would have been described by me many months ago had it not been necessary to compare it with other species as rare as they were obscure. The kindness of the authorities at the Imperial University and at the Academy of Sciences in St. Petersburg, the Museum of Practical Geology in London, and, most of all, at the Geological Survey in Ottawa, has enabled me to make a fairly satisfactory study of the forms that elucidate the Condroz species. In addition to them, I have to thank my friend Professor Otto Jaekel, who had at Berlin another specimen of this species, which he purposed introducing to science in his forthcoming Phylogeny of the Pelmatozoa under the name *Dinocystis Barroisi*; on learning that we had more and better specimens for study he generously waived any objections he might have had to my prior publication.

The ascription of these specimens to the "Psammites du Condroz" is confirmed both by the Berlin specimen and by a statement in Dr. Michel Mourlon's "Géologie de la Belgique" (tome ii, Bruxelles, 1881). A "Liste des fossiles des psammites du Condroz" (p. 23) notes "*Agelacrinus*" as "très-rare" in "Assises de Montfort et d'Évieux," but refers to no published authority for the statement. The "Assises" in question are numbered III and IV by Mourlon, and are the lower two of his divisions of the "psammites" (op. cit., tome i, pp. 92, 93). There is little doubt but that the present species is the *Agelacrinus* of Mourlon.

The "Psammites du Condroz" consist of a micaceous sandstone varying in coarseness, sometimes bluish but, in consequence of weathering, usually brown or even reddish. The calcareous constituents have been leached out, and the fossils occur as either internal casts or external impressions. Unfortunately, the available specimens of *Dinocystis* all belong to the former category. The sandstone may be regarded either as an independent horizon above the Famennian shales and below the Limestone of Etroeungt, or as a littoral equivalent of the typical Famennian shales. The latter view, that adopted by Renevier, is supported by the fact that in the Condroz area the Etroeungt Limestone is replaced by the shales

of Wattignies with *Phacops granulatus, Orthotetes crenistria,* and *Clisiophyllum Omaliusi,* while the shales of Colleret and of Cousobre below the "Psammites" have less thickness than the Famennian shales elsewhere. In either case the "Psammites du Condroz" must be taken as the uppermost member of the true Upper Devonian, the succeeding limestones or shales being regarded as beds of passage to the Carboniferous. The known forms most nearly allied to *Dinocystis* have not as yet been found above the Ordovician.

The Material.

The seven specimens preserved in the British Museum are registered E 7,581 to E 7,587, and may here be termed for short **1**, **2**, **3**, etc., respectively. Of these **2** is selected as holotype, while **1** and **3**–**7** constitute the paratypes.

All are internal casts; but **3** and **7** had small portions of matrix adherent to the under side, and these, being broken away, show parts of the impression.

In outline, as seen from above, the fossils are roughly elliptical, but the orientation of the ellipse varies. A line drawn through anus and actinal pole, and called the antero-posterior axis, almost coincides with the long diameter of the ellipse in **1**, **2**, and **6**; in **3** the long diameter is shifted in the direction of the clock-hand about 25°; in **4** about 35°; in **5** about 20°; while in **7** the shift is contrary to the clock-hand about 75°. The measurements of the diameters of the ellipse, in millimetres, are:—

1	2	3	4	5	6	7
43	38·5	35	32·5	30	28·5	24
38·5	31	26·5	27·5	22	23·5	21

Distance of actinal pole from posterior margin, in millimetres:—

1	2	3	4	5	6	7
19·5	16	12·5	12	12	16	14

These measurements show that the present shape of the specimens is probably due to contortion after death, whether before or after the consolidation of the matrix. But they further suggest that the tendency was for elongation to take place in an antero-posterior direction, and that in life as in death the actinal centre lay posterior to the geometric centre. To confirm these suggestions there is needed a larger series of specimens, and information concerning their relations to the rock-masses in the field.

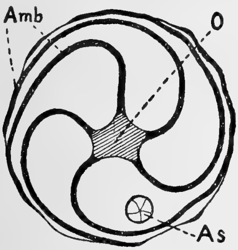
Description of the Species on the Evidence of the Seven Specimens.

One may compare the fossil in a rough way to a Tam-o'-Shanter cap or a Breton béret.

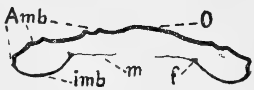
The periphery was approximately circular, varying in diameter from 41 mm. (**1**) to 22 mm. (**7**).

From the periphery, the test curved gently over to the upper surface, and rolled gently inwards on the under surface towards

what would correspond to the opening of the cap. Thus the under surface is hollowed, but since the central region is always filled by matrix one cannot ascertain its structure in full (Pl. XXI, Figs. 1*b*, 2*b*). If the fossil be placed on a flat surface, the actinal pole reaches a height of 14 mm. (**1**), 9 mm. (**2**), 9·5 mm. (**4** and **6**), 6 mm. (**7**). But, owing to the concavity of the under surface, the thickest portion of the actual specimen would be slightly less and would lie about half-way between the actinal pole and the periphery. (Diagram 2.)



1.



2.

DIAGRAMS OF DINOCYSTIS.

(1) The upper or actinal surface.
(2) Vertical section across the middle of the test (based chiefly on **3** and **7**).

O, the actinal pole; *Amb*, the five grooves radiating therefrom and passing over the periphery; *As*, anus; *f*, frame of abactinal surface; *imb*, imbricated peripheral area of same; *m*, thin membrane of central area of same.

On the Upper Surface, from the actinal pole, five Radial Grooves pass outwards over the test, each curving as it goes in a sinistral or contra-solar direction (Diagram 1). Each reaches the periphery, and passes along it for fully a fifth of the circumference, or may even pass over to the under surface, so that in nearly all the specimens one or more of the grooves is visible from below.

Apart from the contortion of the specimens, the grooves are not wholly dominated by pentamerous symmetry. They show the primitive division into one anterior, and two pairs of lateral grooves, and are besides not quite regular in their course.

The grooves, as seen on the internal casts, are clearly marked channels, deeper and narrower towards the periphery, where they have undergone more compression. They are bordered on each side by a row of equidistant small knobs, which become smaller distalwards; the knobs are either opposite each other or slightly alternating, and each pair is connected by a faint ridge (Figs. 1*c* and 2*d*). A wax squeeze shows that this appearance is due to the former presence of plates flooring the groove (Figs. 2*e* and *f*). It is probable that these plates originally were in two alternating rows, but that they usually came to lie in pairs without alternation. They may even have fused (as was perhaps also the case in *Haplocystis* Roemer); at any rate there is no sign of a median suture. Between successive plates, on each side, was a pore, represented in the

internal cast by a knob. Of these pores from three to six may be counted in 5 mm., according to the distance from the ambulacral centre (**2**). (Figs. 2*e, f.*)

A flattened, elevated, roughly pentagonal area over the actinal pole in **1**, **3**, and **5**, may indicate that this was roofed in by covering-plates. Such a structure may also be inferred from the evidence of allied genera. The covering-plates that doubtless once roofed in the rest of the grooves, were probably removed before fossilization.

The Interradial Areas of the upper surface form slightly concave depressions between the radial grooves. They were covered with polygonal plates (about $2{\cdot}5 \times 2$ mm., or less), having their longer diameters parallel to the grooves; there is no evidence that these plates overlapped each other.

In the interradius which (for that reason) has been here termed 'posterior,' lay the anal opening, surrounded apparently by minute plates, the number of which cannot be ascertained. The representation in Diagram 1 is purely diagrammatic. The rounded anal eminence can be recognized on all the casts, at a varying distance from the actinal centre and from the periphery. This interradius is wider than the others near the actinal pole, and in that region probably lay the hydropore. The interradial areas are really continuous with the test of the under surface; but practically they are separated, partly by the almost complete encircling of the periphery by the radial grooves, partly by a rather sudden change in the structure of the test.

The Under, or Abactinal Surface, was divided into two areas, an inner or central, and an outer or peripheral, by a circular Frame, corresponding in position to the rim of a Tam-o'-Shanter, but turned inwards and slightly upwards, not downwards (Diagram 2), Evidence for this frame is presented by specimens **2**, **4**, **3**, and **7**. especially the two latter, which had this region protected by matrix. Removal of the matrix, or cutting across it (Fig. 7*b*), shows a distinct space, triangular in section, encircling the central area. This can only be accounted for by supposing that thicker calcareous plates existed here, and have been dissolved away (cf. Figs. 7*c*, 7*d*).

Peripheral Area.—The frame was depressed to about half the total thickness of the animal, and between it and the periphery there rolled convexly a somewhat flexible integument in which were set minute narrow plates, with their long axes at right angles to the radii of the circle. The edges of these plates appear to have projected outward, towards the periphery of the test, so as to produce an imbrication (**1**, **2**, **3**, **4**, **7**). Flexibility is ascribed to this area chiefly on the evidence of **2**, which shows a radial folding in places.

Central Area.—What was inside the frame cannot be determined satisfactorily. There are in **2**, **3**, and possibly in others, suggestions of a fine and flexible membrane stretched loosely across the opening of the frame. Traces of this are only seen near the edge, and there is no proof that it was continuous. In **2**, however, the visible traces show a fine radial pleating, such as might have been produced, had the membrane been continuous, by some pressure in the central region. (Fig. 2*b*.)

Systematic Position.

Discussion of the meaning of the above-mentioned structures, and of the affinities of the genus, must be postponed until *Edrioaster* has been decently described and figured. I may, however, anticipate by saying that the Condroz form is clearly a close ally of *Edrioaster*, but that it may be distinguished from that genus, as now known, by the tenuity and flexibility of the peripheral area of the abactinal surface, which area in *Edrioaster* is formed of plates no less solid than those in the interradial areas of the actinal surface.

Edrioaster and *Dinocystis* may be separated from the Agelacrinidæ and Cyathocystidæ, as a family Edrioasteridæ, by the absence of a definite border defining the actinal surface, and by the passage of the radial grooves on to the abactinal surface. We may therefore give the following diagnosis of

Dinocystis,[1] gen. nov.

An Edrioasterid with the peripheral region of the abactinal surface composed of a thin flexible integument containing narrow imbricating ossicles.

Genotype : *D. Barroisi*,[2] sp. nov. (= *Agelacrinus*, sp., Mourlon), Upper Devonian, Psammites du Condroz, Belgium.

The characters of the species are of course those of the above description, but one may allude specially to the relatively narrow radial grooves, and to their consistent sinistral curvature. The holotype is in the British Museum, registered E 7,582.

EXPLANATION OF PLATE XXI.

Dinocystis Barroisi.

[All the drawings are from specimens in the British Museum. Figures 1*a*, 1*b*, 2*a*, 2*c*, 3, 4, 5, 6*a*, 6*b* are based on photographs by Mr. J. Green; the other figures are by Mr. G. C. Chubb. All figures are natural size, except 1*c*, 2*d*, 2*e*, 2*f*, which are × 4 diam., 7*b*, which is × $\frac{3}{2}$, and 7*c* and 7*d*, which are × 2 diam. In all the complete views the right and left of the specimen correspond with the right and left of the observer.]

Fig. 1 (E 7,581). *a*. Actinal surface ; anus distinct in lower interradius.
- *b*. Abactinal surface ; radial grooves are seen at top and on left ; imbricating plates of peripheral area well shown.
- *c*. Distal portion of a radial groove drawn from the specimen.

Fig. 2 (E 7,582). *a*. Actinal surface ; impressions of interradial plates are clear.
- *b*. Seen from anterior end ; the groove in the middle is anterior.
- *c*. Abactinal surface ; the trace of the frame is seen between east and south of the drawing ; the coarse radial folding of the peripheral area and the fine folding of the central area are seen between S. and S.S.W. ; portions of radial grooves are visible at both top and bottom.
- *d*. Portion of anterior radial groove, drawn from specimen just where the groove first curves sharply to the left in Fig. 2*a* ; shows knobs and transverse ridges.

[1] Δεινός, *terrible, wondrous*. It might astonish anyone not acquainted with the true structure of *Edrioaster*.

[2] In honour of Dr. Charles Barrois, whose valuable work on Devonian rocks and fossils, of other districts, must be held to excuse this dedication to him of a fossil with which he has had no obvious connection. The undesirability of applying the names of persons to species, without cogent reason, has been maintained by me so consistently that it will be understood that these names, suggested by Dr. Jaekel, are here adopted merely so as to avoid any possible confusion.

e. Wax squeeze of the same; showing pores and flooring-plates of the groove as they would appear on the inside of the test.

f. Similar squeeze from a part of the groove nearer the periphery, showing the twisting over of the flooring-plates.

FIG. 3 (E 7,583). Actinal surface; the crack running from N.E. to S.W. shows the fracture that enabled the transverse section, Diagram 2, to be reconstructed.

FIG. 4 (E 7,584). Abactinal surface; shows imbrication of peripheral area, and traces of the frame.

FIG. 5 (E 7,585). Actinal surface; the pentagonal area at the actinal pole is well marked, owing to the breaking away of the portion of the cast that represented the covering-plates.

FIG. 6 (E 7,586). *a.* Actinal surface.

b. Abactinal surface; shows large central hollow and traces of frame.

FIG. 7 (E 7,587). *a.* Actinal surface; the line *x—y* is that of the section *b*; this latter shows the trace of the frame in the left half.

c Portion of abactinal surface of specimen, showing marked trace of the frame.

d. Wax squeeze from impression of same in matrix, therefore representing outside of test; shows imbricating plates more distinctly, but trace of frame far less distinctly.

NOTE ON *DINOCYSTIS BARROISI.*

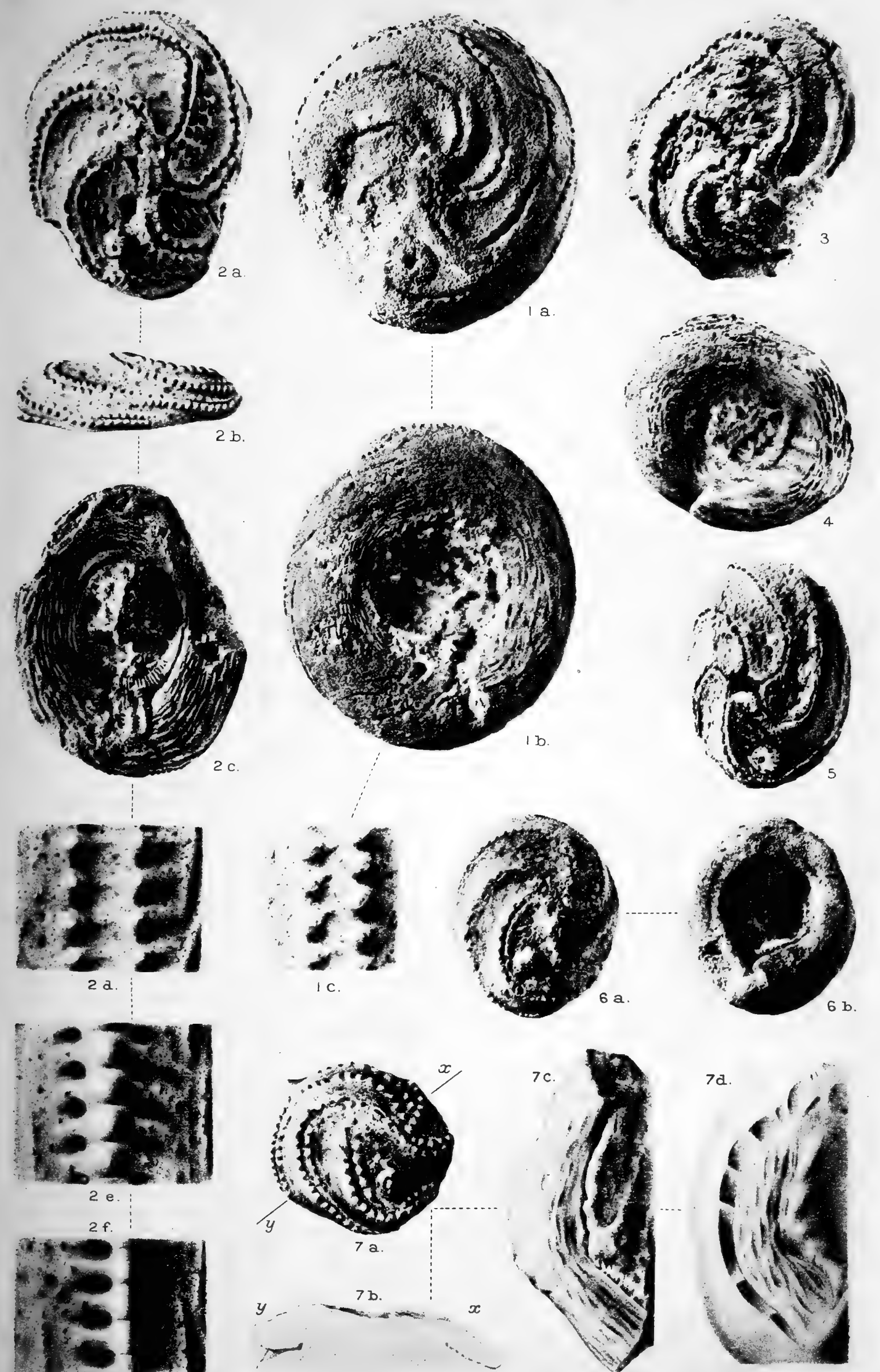
[GEOL. MAG., N.S., Dec. IV, Vol. VI, p. 94; Feb., 1899.]

SIR,—Please allow me a few words in reply to the valuable paper of Mr. F. A. Bather on *Dinocystis Barroisi.*[1] In his paper "Sur l'étage devonien des psammites du Condroz en Condroz" (Bull. Acad. des Sci. de Belg., 1875, 2e sér., t. xxxix, pp. 658–9), Mr. M. Mourlon mentions, from Mr. Malaise's collection, an "astérie" found near Walcourt in an indeterminate "assise" of the "psammites du Condroz." This fossil is no longer quoted in the list of the fossils of this series, given by the same author in his "Géologie de la Belgique," but it is replaced (t. ii, p. 23) by *Agelacrinus,* very rare, in the "assises" of Montford and Évieux, the two *upper* assises of our Psammites du Condroz, and this is supposed by Mr. Bather to be the same as his *Dinocystis Barroisi.* Now the "astérie" of 1875 is the species found by Mr. L. Bayet, and described by me in my "Fragments paléontologiques" (Ann. Soc. géol. de Belg., 1881, t. viii, Mém., pp. 52–54, pl. iii, figs. 1 et 2), under the name of *Protaster Decheni,* and for important reasons I believe that the *Agelacrinus* of 1881 is the same species. Recently, I have learned from Mr. L. Bayet that his fossil was found in the "assise d'Évieux."

G. DEWALQUE.

LIÉGE, *January* 9, 1899.

[1] See GEOL. MAG., Dec. IV, Vol. V, December, 1898, p. 543.



J. Green, Photo. G. C. Chubb, del. London Stereoscopic Co. imp.

DINOCYSTIS BARROISI, 1898.

THE HORIZON OF *DINOCYSTIS BARROISI.*[1]

[GEOL. MAG., N.S., Dec. IV, Vol. VI, pp. 134–136; March, 1899.]

SIR,—Professor G. Dewalque, writing in your February number (N.S., Dec. IV, Vol. VI, p. 94), gently turns the Famennian beds of the Condroz right way up again from the reversed position into which an annoying slip on p. 543 of my paper had thrown them. For this friendly intervention he has my thanks, but with his main thesis I am unable to agree. The question at issue is the horizon of *Dinocystis Barroisi*; to this all the rest is subsidiary. Let us make the question clear by printing the list of the horizons of the Famennian, in descending order, as given in "Légende de la Carte Géologique de Belgique, etc.," 8vo, Bruxelles, 1896.

DEVONIEN SUPÉRIEUR.

Famennien supérieur.

Assise de Comblain-au-Pont [=Etroeungt Limestone].
Assise d'Evieux.
Assise de Monfort.
Assise de Souverain-Pré.

Famennien inférieur.

Assise d'Esneux.
Assise de Mariembourg.
Assise de Senzeilles.

This list does not imply an absolute vertical succession: it appears, for instance, that the Assise d'Evieux, with its rich flora, may be a more littoral facies of the Assise de Monfort, while the Assise

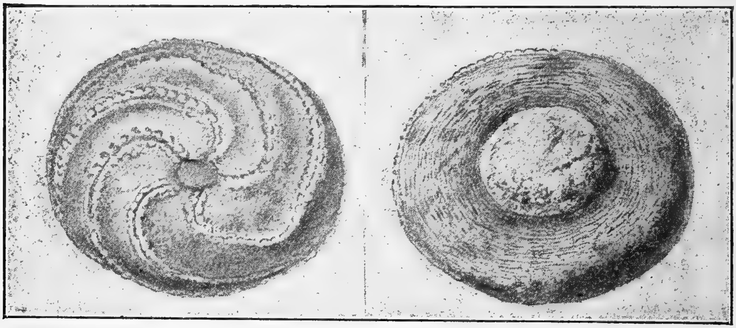
[1] See GEOL. MAG., N.S., Dec. IV, Vol. V, pp. 543–8 (December, 1898). Footnote 1 on p. 547 explained the name *Dinocystis* as derived from δεινός, *terrible.* Although this seemed peculiar, it did not occur to me that Dr. Jaekel must have intended to derive it from δινεῖν, *to whirl round,* in allusion to the marked curvature of the radial grooves. Thus regarded, the name is highly appropriate.

d'Esneux may be the arenaceous equivalent of the more shaly beds of Mariembourg.

Now my argument was that *Dinocystis Barroisi*, being what was usually called an *Agelacrinus*, was with little doubt the same as the "*Agelacrinus*" which Mourlon cited in 1881 ("Géol. de la Belgique," ii, p. 23) from "Assises de Montfort et d'Evieux"; and therefore that our specimens of *D. Barroisi* also came from these beds, "the uppermost member of the true Upper Devonian." Professor Dewalque states that, "for important reasons," he believes the *Agelacrinus* of Mourlon, 1881, to be the same species as a certain "astérie," to which Mr. Mourlon referred in 1875 as being in "collection Malaise." This "astérie," according to Prof. Dewalque, is a specimen of his *Protaster Decheni*, from the Assise d'Evieux. If these beliefs were justified, it would follow that *Dinocystis Barroisi* was not the same as the *Agelacrinus* of Mourlon, and it would be referred to the same horizon on no better evidence than an inaccurate dealer's label.

Since the validity of Professor Dewalque's criticism entirely depends on "important reasons," we should be warranted in disregarding it until those reasons have been published. But the high authority of my critic, no less than the difficulty of attributing so incomprehensible an error to the learned director of the Service Géologique de Belgique, has led me to investigate the question afresh.

The results more than justify my former inference.



Dinocystis Barroisi: photographic reproduction (reduced to $\frac{8}{9}$) of a pencil-drawing made for Mr. Mourlon in 1881, from the specimen then referred by him to *Agelacrinus*. The position of the anus was not observed by the draughtsman; it may well have been in the rather irregular interradius to the right in the drawing of the actinal surface.

Professor C. Malaise kindly informs me that the above-mentioned "astérie" is still in his collection, that it is a specimen of *Protaster Decheni*, Dewalque, and that the bed at Walcourt from which it came belongs, in his opinion, to the Assise d'Esneux (not the Assise d'Evieux, to which the type-specimen is now referred).

Mr. Mourlon most courteously sends me a drawing, here reproduced, of the specimen mentioned by him as "*Agelacrinus*" in 1881. It is not the "astérie" of Professor Malaise; it is not a *Protaster Decheni*, or any kin thereto; but it is a fine specimen of an Edrioasteroid, as large as, and more perfect than, the British Museum specimen E 7581, with actinal and abactinal surfaces clearly shown; and it belongs incontestably to *Dinocystis Barroisi*. F. A. Bather.

British Museum (Natural History).
February 5, 1899.

II. *Edrioaster Buchianus* Forbes sp.

[Geol. Mag., n.s., Dec. IV, Vol. VII, pp. 193–204, Pls. VIII, IX, X; May, 1900.]

In 1848, under the name *Agelacrinites Buchianus*, Edward Forbes introduced to science "one of the most remarkable Cystideans as yet discovered in British strata." His description and figures, published in his memoir "On the Cystideæ of the Silurian rocks of the British Islands" (Mem. Geol. Surv. Gt. Brit., II, pt. ii; see pp. 519–523, and pl. xxiii), have not proved fully intelligible to subsequent workers, even to those who have had the fossil before them. Unfortunately J. W. Salter, in his "Appendix. On the Fossils of North Wales," to "The Geology of North Wales" by A. C. Ramsay (Mem. Geol. Surv. Gt. Brit., III, 1st ed., 1866), criticised a little, but illuminated less; while the same Appendix in the second edition, 1881, though "greatly enlarged and partly rearranged by Robert Etheridge, F.R.S.," merely introduced verbal alterations into Salter's account.

Allusions to this fossil by writers who have not themselves examined it serve chiefly to show the need that exists for a fresh description. Through the kindness of the Director-General of the Geological Survey and of Mr. E. T. Newton, to whom my sincere thanks are here offered, the original specimens were placed at my disposal for several months. About two years ago the first draft of this paper and some of the illustrations were sent to Dr. Otto Jaekel in Berlin, and have been utilised on pp. 44–46 of his splendid volume "Stammesgeschichte der Pelmatozoen. I. Thecoidea und Cystoidea" (1899). Thanks to Mr. J. F. Whiteaves and the Director of the Canadian Geological Survey, I subsequently learned the true structure of *Edrioaster Bigsbyi*, which was unknown to Dr. Jaekel when he wrote the pages referred to. Hence some interpretations in the present account differ from those given by Dr. Jaekel. They agree, however, with the statements in chapter xii—The Edrioasteroidea—of "A Treatise on Zoology, Part III, The Echinoderma," edited by Professor E. Ray Lankester

(London, 1900). Some of the points will be better understood after publication of Study III, which will deal with *E. Bigsbyi.*

The terms used and the arrangement followed in the present account are the same as those in Study I. *Dinocystis Barroisi.*[1]

Horizon and Locality.

The specimens preserved under this name in the Museum of Practical Geology, V $\frac{3}{77}$, were obtained during the summer of 1847 from the Caradoc beds, two miles west of Ysputty Evan; that is to say, about two miles south of Pentre Voelas, and therefore in Denbighshire and not in Caernarvonshire as stated by J. W. Salter (op. cit., 1866, p. 262) and by R. Etheridge, sen. (op. cit., 1881, pp. 395 and 407). Mr. Etheridge informs me that the specimens were not found *in situ*, but were collected by Mr. Gibbs from a wall of loose stones, all of the same material. There seems, however, no reason to doubt that they came from the Caradoc beds of some quarry in the immediate vicinity, for they have the well-known characters of those beds. The matrix is an indurated sandstone, hardly to be described as "schistose" in any modern sense of the word. It contains remains of crinoid stems, brachiopods, and corals; the calcareous portions of these have been dissolved from the outer portions of the stone, and the same is the case with the edrioasteroid.

Description of the Type-Specimen.

This consists of an *internal cast* of the whole individual (Pl. VIII) and an *external impression* of its abactinal surface (Pl. IX). There is also preserved, in the central region of the abactinal surface of the cast (Pl. VIII, Fig. 3), a small portion of the original theca. Except when said to be otherwise, the statements refer to the internal cast.

The periphery is subpentagonal; the sides of the pentagon correspond to the interradial areas, and are slightly convex. The length along the sagittal plane is 36 mm. The transverse diameter is 32 mm.[2] The greatest width of each side is about 20 mm.

From the periphery, the theca rises rather steeply, then curves gently over to a slight depression around the actinal pole; towards the under surface it bends more suddenly. Seen from the side (Pl. VIII, Fig. 2) the theca looks like a round cap squashed in at the top. If the fossil be placed on a flat surface, it reaches a height of 18·5 mm.; but the actinal pole is about 3·5 mm. below this. The under surface is excavate to about 5 mm., so that the length of the polar axis is about 10 mm. The specimen does not appear to have undergone more compression along this axis than it was capable of effecting spontaneously during life.

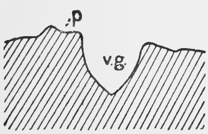
[1] Geol. Mag., n.s., Dec. IV, Vol. V, pp. 543–548, pl. xxi; Dec., 1898.

[2] To dispel possible perplexity, it may be said at once that Forbes' measurements are very inaccurate, sometimes inexplicably so.

On the Upper Surface (Pl. VIII, Fig. 1), five Radial Grooves proceed fairly straight to a distance of 13 mm. from the actinal pole. They then rather suddenly bend in a dextral or solar direction, and, at about 34 mm. from the actinal pole, pass on to the under surface of the theca (Pl. VIII, Figs. 2 and 3); here they continue along the edge until they have attained a distance of about 46 mm. from the actinal pole, when they terminate. The width of a groove in the proximal half of its course is 5·5 to 6 mm.; where it bends over to the underside, the width is about 5 mm., and gradually tapers to 2·5 or 2 mm., after which it is rapidly rounded off.

Of the five grooves, the anterior is the most perfectly preserved. In its proximal half it forms a rather deep V with slightly concave sides, as shown in section, Fig. 1. On the sides are ridges, passing outwards from the median line at an angle that varies with the curvature of the groove, but is never far from a right angle (Pl. X, Fig. 6). These ridges represent the sutures between the flooring-plates. Each ridge passes up to a prominence of somewhat ovoid outline, broader at the end next the groove; the side of the prominence towards the actinal pole has a gentler slope than the side away from it, so that the prominence as a whole seems to pass outwards in an abactinal direction. The depression between adjacent prominences is continued as an exceedingly slight concavity down the side of the groove to the middle line; slight though it be, it is observable in some parts where the sutural ridges on either side cannot be detected. The prominences, and consequently the sutural lines, on the two sides of the groove do not actually alternate; neither do they quite correspond. Therefore the ridge that may, in places, be seen at the bottom of the groove, representing the suture between the flooring-plates of the two sides, bends alternately to either side; in the tract figured (Pl. X, Fig. 6), a long stretch towards the right (of the figure) is followed by a short stretch towards the left.

Fig. 1.



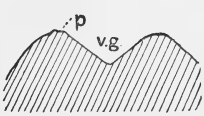


Fig. 2.

Sections across the internal cast of the anterior groove, both as seen from the oral side; × 4 diam. *v.g.* impression left by flooring-plates of subvective groove. *p.* matrix rising up into the pore between adjoining flooring-plates.

Fig. 1, from proximal region of groove.

Fig. 2, from more distal region, just on the periphery or ambitus of the fossil.

The distal region of any groove deviates from the structure just described only in the proportionately less depth of the groove, in the more pronounced alternation of the plates, and in the relative elongation of the prominences, which here merge more gradually into the sutural ridges. (See section of cast, Fig. 2).

A wax squeeze taken from the impression of the distal region of a groove (e.g. the left posterior, Pl. X, Fig. 7) restores the appearance

formerly presented by the now vanished test as seen from the outside. In this region we see the flooring-plates rising slightly above the interradial areas, then presenting a narrow flat surface, then dipping down in a slightly convex curve to the middle line of the groove. The groove is less deep than in the internal cast, which means that the flooring-plates were thicker in the middle of the groove than at its margins. Between the flooring-plates, where they bend downwards, are elongate slits, wider towards the margins of the groove; these correspond to the prominences of the internal cast.

The right anterior and left posterior grooves are still filled in places by portions of matrix; and the hollows between this matrix and the internal cast enable one to reconstruct a section of the groove based on actual measurement. Fig. 3 is taken from the left

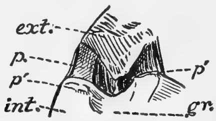


FIG. 3.—View of the left posterior groove, as preserved in the fossil. × 4 diam. *ext.* matrix filling the exterior of the groove. *int.* matrix filling the interior of the test. *gr.* groove on the surface of the latter. *p.* matrix filling pores between the flooring-plates. *p'.* scars where the same has been broken away.

posterior groove, at 5·5 mm. from its distal end. Here the plates are about 1 mm. thick at the edge of the groove, but thin considerably towards the middle line.

A good idea of the appearance of the groove as seen from the inside of the test is obtained from a wax squeeze of the internal cast (Pl. X, Fig. 5).

Forbes describes the "margin of the" grooves as composed of "areal or interambulacral plates bearing 2–3 short elevated transverse ridges, each of which points to the origin of an ambulacral plate, short and oblong; a double series of these ambulacral plates form the canal." It is hard to believe that Forbes did not understand he was dealing with an internal cast; yet this seems to have been the case, for he proceeds to describe the external impressions of the grooves as triangular arms "composed of two rows of dove-tailing joints, with ridges at the articulations to lock into the furrows bordering the arm-canal." From this truly remarkable misconception arose an extraordinary theory as to the nature of the radial grooves and as to the homologies of the ambulacral areas in Echinoids. After half a century one need not linger over mere errors of fact in the first sentence quoted. The present description and figures will enable readers to make the corrections themselves.

Piecing all this evidence together as in Fig. 4, we see that each radial groove was composed of a double row of flooring-plates, more or less alternating, and meeting in a median zigzag line. In the proximal half of the groove the long axis of each of these plates, nearly at right angles to the middle line of the groove, measured 3–3·5 mm., and the short axis, parallel to the middle line, ·9 mm. The total number of plates along one side of a groove was about 60

(certainly more than the 50 which Forbes counted). The thickness of the plates towards their outer margins was about 1 mm. The plates were continuous with the interradial thecal plates, but rather thicker; at a little distance from the edge, they bent downwards at a rather sharp angle, so as to form a V-shaped trench with slightly convex sides. Seen from the inside the plates formed a ridge, with sides at first steep, then gradually rounding over.

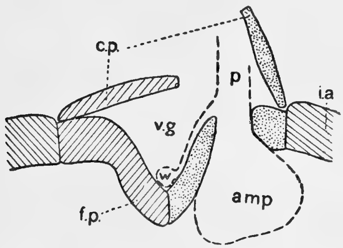


Fig. 4.—Reconstructed section across a subvective groove. × 6 diam. Compare with Fig. 1 on p. 195, and Fig. 3 on p. 196. The relations of the covering-plates are inferred from *Edrioaster Bigsbyi*. The position of the perradial water-vessel and its branch to the podium is deduced from the remains of *E. Bigsbyi* and the present species. Natural suture-surfaces are dotted; cut surfaces are ruled diagonally; supposed soft parts are in broken outline. *v.g.* subvective groove. *c.p.* covering-plates. *f.p.* flooring-plates. *i.a.* interambulacrals. *w.* perradial water-vessel, connected by a branch with the podium, *p.* *amp.* ampulla connected with the podium through the pore.

The adjacent sides of the plates were excavate so that pores were formed between them. Thus the groove was fringed with a row of pores on either side. These pores lay, not at the extreme margin, but just where the plates bent downwards; they passed outwards at an angle sloped away from the actinal centre; they were wider in the proximal portion of the groove, and more elongate in the distal portion. We may infer from the as yet undescribed structure of *Edrioaster Bigsbyi*, that the groove was roofed by covering-plates, which rested on the flattened border. But these covering-plates must have been detached and washed away before the theca was imbedded, since no traces of them remain.

Around the Actinal Pole the form of the internal cast is rather complicated (Pl. X, Fig. 2). The grooves curve down towards the pole, and at 2 or 3 mm. from the pole itself they bend downwards sharply. The central region is occupied by an irregularly shaped mass of matrix, with a broken surface about 3·5 mm. below the highest point of the cast. This mass probably represents the œsophagus. It is surrounded by a channel or, as it were, a moat, into which the down-bent grooves lead. At certain points, however, this moat is bridged by matrix, and in the two rays of the left side the extreme proximal ends of the grooves are similarly bridged. These bridges look like continuations of the prominences or infillings of the proximal pores. In the posterior interradius is a similar lump of matrix, mistakenly alluded to by Forbes (op. cit., p. 522) as "the projection which bore the anus." This is separated from the œsophageal

matrix by the moat, and is itself bordered on its outer side by a semicircular channel, which dips down on each side to join the moat; just at those points, this channel is very nearly bridged by projections from its enclosed matrix almost joining the proximal prominences of the adjacent rays. Owing to the bridging and overhanging of the matrix, it is impossible to obtain a satisfactory wax squeeze of the channels; but, translating the appearances into the original stereom structures, we infer that the mouth was central and roughly five-lobed, widest on the posterior side, and that it was surrounded by a stout ring of stereom, over which the food-grooves passed. This latter structure may possibly be that described by Salter (op. cit., p. 291) as "a great thickening of the oral ossicles, just within the mouth." The proximal or adoral pores were connected with one another above this stereom ring, but below the outer theca, so as to form a closed ring-canal (hydrocircus) around the mouth. In the posterior interradius was a madreporite or hydropore-plate, the inner surface of which formed a semicircular projection for the attachment of the upper end of the stone-canal. This was more or less directly connected with the ring-canal. The existence of pores along the radial grooves almost certainly implies the presence of podia, as well as of perradial water-vessels connecting the latter with the ring-canal. But the specimen does not afford satisfactory evidence as to the position of the perradial vessels.

The shape of the Interradial Areas has been figured by Forbes (op. cit., pl. xxiii, fig. 5), but the arrangement of the plates thus represented, though not ridiculous, is imaginary so far as details are concerned. His drawing, however, presents a certain resemblance to the left anterior interradial area, here refigured (Fig. 5). This

Fig. 5.

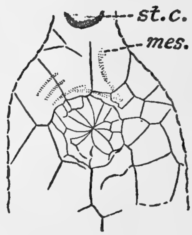


Fig. 6.

Fig. 5.—Arrangement of plates in left anterior interradius. Nat. size.
Fig. 6.—Arrangement of plates in upper part of posterior interradius. Nat. size. *st.c.* depression caused by stone-canal. *mes.* depression perhaps caused by mesentery.

shows the marks left by the plates pretty clearly, and indicates that they were irregular polygons of various sizes, apparently not imbricate. The only regularity visible in their arrangement here is a band of plates bordering the right side of the area, and passing across it at the lower edge of the theca, while another less regular band runs parallel to, and on the inner or left side of, this outer one. Down to and including these bands, there were 36 plates in the left anterior interradial area. The greatest width of this

area is 13·75 mm.; that of the posterior area is 16·5 mm. The latter also tapers less rapidly towards its actinal end, where the hydropore was situated.

The greater width of the posterior interradial area (Fig. 6 and Pl. VIII, Fig. 1) is due to the anal opening, which lay in this area about half a millimetre to the left of its middle line and at 11 mm. from the actinal pole. The anal pyramid ("ovarian pyramid" of Forbes) was not a regularly constructed pyramid surrounded by a definite rim, but was a roughly circular area of about 6·25 mm. in diameter, the plates of which appear to have risen from under the edges of the surrounding interradials. The plates contained within this circle seem to have been irregularly disposed in two circlets. The plates of the outer circlet were not so long as those of the inner. These latter were roughly triangular and met in a central point, where doubtless was the anus; the sutures indicate their number as 11, although Forbes estimated them at only 5. The anal pyramid can hardly be described as raised; but above it, and half surrounding it, is a semicircular depression with three concentric wrinkles plainly marked on its left side. Immediately on the right of the anus, the test is not depressed. In the adjacent (r. post.) interradius there is a slight elevation of the theca at this level, clearly shown in the side-view (Pl. VIII, Fig. 2). The wrinkled depression in the anal interradius may be ascribed to the contraction after death of some internal structure, presumably the mesentery attaching the stone-canal to the theca. The slight swelling that curves round from the anus may indicate the course of the rectum; and this would imply that the gut had a dextral coil. Jaekel also has expressed this view (op. cit., p. 46).

The Under or Abactinal Surface of the theca (Pl. VIII, Fig. 3, and Pl. IX) is partly bounded by the dextrally curved ends of the radial grooves, which, as seen from below, of course appear sinistral. The excavate space included by these may be divided into three regions, which, proceeding from without inwards (i.e. from oral to aboral), are as follows :—

(1) Peripheral Area.—A closed ring formed by small polygonal plates like the interradials, with which they are in fact serially homologous. These plates are roughly arranged in rows continuing the spiral twist of the grooves. They are a little smaller than the majority of the interradials, and their long axes are directed more or less radially to the vertical axis of the theca.

(2) The Frame.—A closed ring of 11 thicker and larger plates, with their long axes tangential to the vertical axis of the theca. Their outer margins are slightly scolloped by the sutures with the plates of the peripheral area; the inner margin of each forms a curve, convex towards the aboral pole. These plates seem to alternate in size, a smaller plate corresponding to each interradius and a larger to each radius. Two plates go to the wider posterior area. Too much stress, however, must not be laid on this slight appearance of regularity. These plates were ornamented with small tubercles, the traces of which are seen on both the cast and

the impression, more pronounced than those left by the interradials of the actinal surface.

(3) Central Area.—The whole space within the frame is still covered in the cast by what appears to have been a flexible

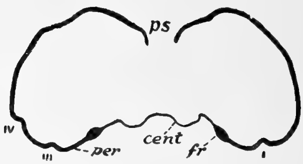


Fig. 7.—General section across the theca of *Edrioaster Buchianus*, about in the transversal plane. Natural size. i, iii, iv, three subvective grooves (compare Plate VIII). *ps.* peristome, the thickening of the circumœsophageal ring not shown. *per.* peripheral area of the abactinal surface. *cent.* central area of same. *fr.* frame surrounding the latter.

integument, in which were deposited minute, loosely calcified, imbricating plates. The imbrication is such that the outer edges of the plates are directed away from the abactinal pole. The exact arrangement of this, and its relation to the surrounding plates, are, however, best made out from a wax squeeze (Pl. X, Figs. 1 and 8) of the impression (Pl. IX).

Forbes speaks of this central portion as a "tough membrane," over which "from the centre radiating lines, with the appearance of having been caused by vessels, proceed, dividing in their course . . . The markings . . . resemble those of *Ischadites.*" There can be no doubt, now that we know the structure of other Agelacrinidæ so much better than Forbes could, that these lines are merely the edges of imbricating plates. This was fully recognised by Salter (op. cit., p. 291).

Forbes' view is here mentioned in order to explain his next sentence. "The plates immediately bordering it [the membrane] are rather larger than the others, and all the plates of the base are marked with twin pore-like dots, connected by a groove." By "all the plates of the base" we must understand, not the minute imbricating plates of the membrane, but the 11 plates forming the frame, and the smaller plates of the peripheral area. Forbes' pl. xxiii, fig. 7, shows these diplopores on one of the frame-plates, but not on the membrane, while the peripheral plates are only drawn in outline. I have been quite unable to distinguish any structure at all resembling the diplopores so clearly described and figured by Forbes; there is nothing more than the tuberculation already referred to. Salter says, "The surface of the plates [in general] is granular, but I can see no trace of spines; nor can I see the chain-like pairs of pores on the puckered membrane, as figured by Forbes in his fig. 7. I think the artist has been deceived by the imbrication of the small calcareous plates which covered this surface." The chief conclusion to be drawn from these bewildering remarks is that Salter did not take the trouble to understand the clear description and figure of his predecessor. Salter's statement,

however, was repeated in modified language by Etheridge (op. cit., p. 482), and it may therefore be considered that two palæontologists of repute were, as I am, unable to see the diplopores described by Forbes and drawn by C. R. Bone.

The most important features of the abactinal membrane are 5 prominences or evaginations of it. They form a fairly regular pentagon, each corresponding to an interradius, but they bear no evident relation to the angles of the central area. Each evagination has a rounded U-shaped margin, the apex directed away from the thecal axis. The raised margins are not absolutely continuous. Within the margins the membrane is again depressed, and just in the middle, about the actinal pole, it cannot be traced in either cast or impression. Possibly it was here very thin and contained no imbricating calcareous plates. There is, however, no evidence that there was either a stem-attachment, as Forbes thought, or any opening from the gut or the body-cavity to the exterior.

These evaginations of the aboral membrane, alluded to by Forbes as "prominences" (p. 522) and "peduncles" (p. 538), received another explanation from Wyville Thomson.[1] He writes (p. 110): "In the specimen of Agel. Buchianus (Forbes), in Jermyn Street, there is a rudely pentagonal stamp on the apical surface, which is probably the impression of the wide base of a pyramid of jaws like that of Echinocystites, on the inside of the coriaceous integument." This is very incorrectly expressed, and were it not for some remarks by Salter (op. cit., pp. 290, 291), would be unintelligible. By "the pentagonal stamp," Thomson seems to have meant, as Salter says, "the five indentations figured by Forbes, fig. 6," i.e. indentations not on the apical surface, but on the impression of that surface, and therefore not really indentations but prominences. Salter, attempting to improve on Thomson, speaks of them as "large buccal teeth . . . which must, I suppose, represent the 'lantern' in the *Echinus*."

To this interpretation of the prominences there are objections of three distinct kinds. First, the specimen, though it shows traces of the circumoral ring plainly enough, shows within or below this ring no traces whatever of jaws or teeth. Secondly, the buccal armature of *Palæodiscus* would not make an impression of this nature or in this position, while that of *Echinocystis* is not large enough to make any such impression at all.[2] Thirdly, it is inconceivable that an Echinoderm of distinctly pelmatozoan type, with mouth upturned and with deep subvective grooves, can have had any use for stout biting jaws; even if descended from a gnathostomatous Echinoid (a quite absurd supposition) it would have lost its jaws before attaining its present habit and structure.

The meaning of these five extrusions of the aboral membrane must be sought among other Pelmatozoa. They must have been

[1] C. Wyville Thomson, "On a new Palæozoic Group of Echinodermata": Edinburgh New Phil. Journ., N.S., vol. xiii, pp. 106–117, pls. iii, iv; Jan., 1861.
[2] See W. J. Sollas, "On Silurian Echinoidea and Ophiuroidea": Quart. Journ. Geol. Soc., vol. lv, pp. 692–715; Nov., 1899.

made by some system of organs that had undergone division into five, and had the pentameres interradial. The stomach, gonads of Echinoid type, and water-vascular system seem therefore to be excluded, while the chambered organ of crinoids is forcibly suggested.

It is clear that the frame of 11 large plates gave some rigidity to the base, while within this the membrane was very flexible, capable of extension and contraction. These arrangements may have served a twofold purpose. If the theca were compressed by any external agent, the soft parts and the fluid contents of the cœlom would have been squeezed out into this extensile sac, which thus acted as a safety-valve. Or the vertical mesenteries of the cœlom may have been attached to it, and, developing muscles as in Echinothuridæ, may have been able to withdraw it within the frame; if the outer edge of the theca were closely apposed to the ground, the effect of this would be to create a vacuum and so hold the creature in its position like a limpet. In the dead animal, when the tissues shrank, the aboral membrane was naturally pulled upwards, and at the same time other parts of the theca were pulled inwards. Hence arose the stretching of the membrane over the internal (? chambered) organs, in the same way as the wrinkled depression already noticed in the posterior interradius. Jaekel's opinion that the central area of the abactinal surface was fixed (*aufgewachsen*) on a not quite hard bottom, does not seem in accord with the shape of the theca or with the sharp definition of these five lobes.

Other Specimens.

The various stem-fragments ascribed by Forbes to this species can, as already noted by Salter and Etheridge, have had nothing to do with it. They were found in the same stone wall, but not in juxtaposition with the theca. Neither can the 4-rayed impression so badly represented in Forbes' pl. xxiii, fig. 14, be regarded as "the impression of the base, probably of a similar cystidean."

There was found, however, one other fragment, which I am unable to fit on to the type-specimen, and therefore regard as indicating the existence of another individual. It is an impression of part of an ambulacrum, 16 mm. long, and of portions of the adjacent interambulacra, one of which shows very clearly the markings produced by the ornament of the plates (Pl. X, Fig. 3).

No other specimen of this species is known.

Systematic Position.

Forbes called this species *Agelacrinites Buchianus*, comparing it first with the specimen discovered by Bigsby, and described and figured by G. B. Sowerby in the Zoological Journal (vol. ii, pp. 318–320, pl. xi, fig. 5, 1826), and afterwards named *Agelacrinites Dicksoni* by E. Billings (1856); and secondly with *Agelacrinites hamiltonensis*, Vanuxem, which is the type of the genus. Forbes considered it as a Cystid, allied to the Echinoidea.

Salter (op. cit., p. 290), while retaining the species in *Agelacrinus*, considered it as more allied to the species described by Billings as

Edrioaster Bigsbyi, 1858. In the list on p. 262 of the same work it is actually called "*Edrioaster Buchii* (*Agelacrinus*, Forbes)." The same is the case in Etheridge's revision of Salter (pp. 481 and 395).

Salter's opinion is abundantly justified not only by the details of the present paper, but by the new facts concerning *Edrioaster Bigsbyi*, which will form the subject of the next study. To that it is better to postpone the diagnoses of the genus and of the present species.

EXPLANATION OF PLATES VIII, IX, AND X.

Edrioaster Buchianus.

[All the figures are from the type-specimen in the Museum of Practical Geology, except Pl. X, Fig. 3, which is from a fragment associated with it. Plates VIII and IX are based on photographs by Mr. J. Green; the figures of Plate X are drawn directly from the specimens or from wax squeezes thereof. The figures of Plates VIII and IX are magnified two diameters; those of Plate X are enlarged to the extent stated under each. Difficulties of lighting have rendered impossible a rigorous maintenance of the standard orientation; where doubt might have arisen the position of the anal interradius has been marked by a *.]

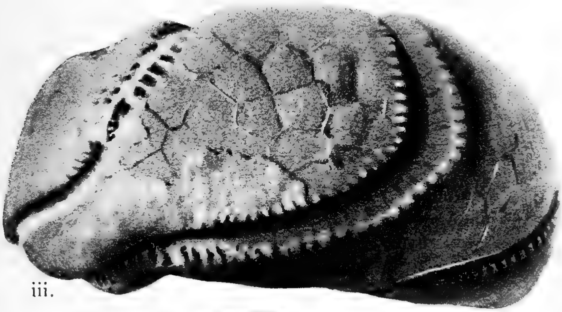
PLATE VIII.—The internal cast.

FIG. 1.—Actinal surface, showing peristomial and anal areas clearly, and the subvective grooves here occupying an almost strictly radial position and marked i–v from left posterior to right posterior.

FIG. 2.—Side view, showing the curvature of the subvective grooves. The anterior groove (iii) passes across the middle of the figure. The plates of the right anterior interradius (between iii and iv) are fairly distinct.

FIG. 3.—Abactinal surface, showing in its central area a portion of the original test (compare Pl. X, Fig. 8). The numbers i–v here correspond to those of Fig. 1, and mark the radii, while the subvective groove corresponding to each number is now seen to have passed through fully one-fifth of the circumference away from it: e.g. the anterior groove (iii of Fig. 1) now comes into the right anterior radius (iv). Close to number ii some matrix fills the groove, and on this is the impression of a columnal of some crinoid or cystid.

1



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3

J. Green, Photo. F.A.B. del. London Stereoscopic Co. imp.

EDRIOASTER BUCHIANUS.

Plate IX.—The external impression of the abactinal surface. The upper figure is lit from the right hand, the lower figure from the left hand. These figures, with Fig. 3 of Pl. VIII, give the evidence on which Pl. X, Fig. 8 is based.

J. Green, Photo. F.A.B. del. London Stereoscopic Co. imp.

EDRIOASTER BUCHIANUS.

PLATE X.—Enlarged details.

FIG. 1.—A wax squeeze from a portion of the impression of the abactinal surface, showing accurately the relation of the plates; × 3 diameters. Compare Forbes, pl. xxiii, fig. 7. *cent.* small plates of the central area. *fr.* a frame-plate. *per.* plates of the perradial area. *s.* suture between two of the latter, apparently crenulate. *gr.* portion of left anterior subvective groove. *col.* columnal lying on matrix that fills a part of this groove.

FIG. 2.—The peristomial region of the internal cast, slightly diagrammatised, and seen from right posterior interradius; × 2 diam. *st.c.* a depression where a semicircular ridge on the inside of the test is supposed to have supported the stone-canal; the matrix within this would thus have underlain the madreporite. *oes.* matrix filling the œsophagus. *c.o.fr.* hollow space surrounding the latter and presumed to have been occupied by a circumœsophageal frame of plates (modified flooring-plates). *w.v.* strands of matrix bridging over the space just mentioned; they seem to be serially homologous with the podial or pore scars, and may represent water-vessels connecting the adoral podia with a circumoral water-ring.

FIG. 3.—Interambulacrals showing vermiculate ornament and raised, slightly crenulate suture-margins. From a wax squeeze of a fragment associated with the type. × $\frac{5}{2}$.

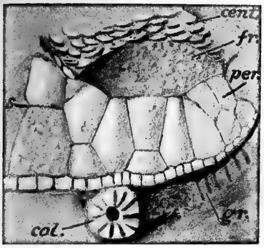
FIG. 4.—Flooring-plates in the distal region of the left anterior groove, drawn from a wax squeeze of the external impression. × 6 diam.

FIG. 5.—Portion of the anterior groove as seen on the inside of the test, drawn from a wax squeeze of the internal cast; × 5 diam. *ia.* interambulacrals. *p.* pores for the passage of the podia or of the ampullæ from the podia. *f.p.* flooring-plates. The proximal end is uppermost in the drawing.

FIG. 6.—The internal cast of part of a subvective groove; the complement of Fig. 5. × 5 diam. *p'.* projecting scars of matrix that filled the podial pores.

FIG. 7.—The distal end of the left posterior groove, from a wax squeeze of the external impression; × 4 diam. Lettering as in Fig. 5.

FIG. 8.—The central part of the abactinal surface, from a wax squeeze of the external cast (Pl. IX), slightly diagrammatised, since details are often obscure in the specimen; × 3 diam. *per.* peripheral area. *fr.* frame. *cent.* central area, with its flexible plated membrane, raised in five interradially situate lobes. * position of posterior (anal) interradius. P.IA. the meridian in which plates of the posterior interradius (i.e. posterior interambulacrals) pass from the actinal to the abactinal surface and merge with the peripheral plates of the latter.



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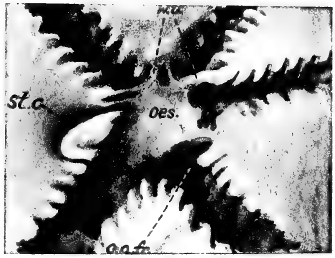

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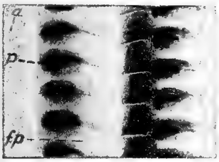

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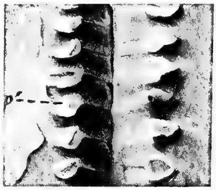

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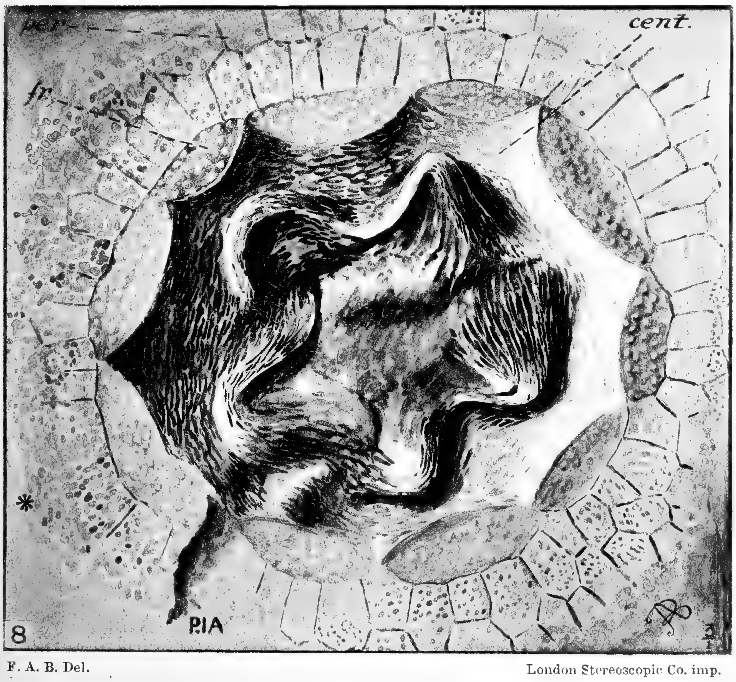

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EDRIOASTER BUCHIANUS.

III. *Lebetodiscus*, n.g. for *Agelacrinites Dicksoni*, Billings.[1]

[Geol. Mag., n.s., Dec. V, Vol. V, pp. 543–550, Pl. XXV; Dec., 1908.]

Previous History.

THE specimen herein to be considered is one of great historical interest, for it was the first specimen of an Edrioasteroid made known to science. It was discovered by Dr. J. J. Bigsby in limestone now recognised as of Lower Trenton age, forming Table Rock at the Chaudière Falls on the Ottawa River at Ottawa (then called Bytown), Canada, in 1822. Brought by Bigsby to England, it was figured and described, though not named, by G. B. Sowerby in 1825.[2] E. Forbes, who had the specimen for study, referred to it in his memoir "On the Cystideæ of the Silurian Rocks of the British Islands,"[3] since the "aspect" of his *Agelacrinites Buchianus* "immediately called [it] to mind"; he even went so far as to say that there could "be no question . . . of its being generically allied" to that species. Considering the not unnatural inadequacy of Sowerby's description and figure, the reputation that Forbes had as an authority on echinoderms, and the comparative imperfection of the first found specimens of *Edrioaster*, it was not surprising that E. Billings in 1856[4] should have supposed a new Trenton fossil, undoubtedly congeneric with *Agelacrinites Buchianus*, to be of the same species as that found by Bigsby, and should therefore have applied to it the trivial name '*Bigsbyi*,' while giving to a fossil of obviously different structure the name '*Agelacrinites Dicksoni*.'[5] In February, 1858, Billings travelled to London with the fossils in question, and found that Bigsby's specimen was not, after all, the same as his *Cyclaster Bigsbyi*, but it was specifically identical with his *A. Dicksoni*. He redescribed the species, and had his type-specimen, as well as Bigsby's fossil, figured by C. R. Bone.[6]

The latter specimen was said by Billings to be then "in the Museum of Practical Geology, Jermyn Street, London." I therefore supposed that it had been transferred to the British Museum when all the foreign fossils were so transferred some years ago. But when no trace of it could be found either in the collections or the registers of that establishment, I applied to Mr. E. T. Newton, palæontologist to the

[1] Publication of the present Study, written in 1899, was delayed owing to an unwillingness to load Zoology with a new generic name without further confirmation from all available evidence. Since that date so much Edrioasteroid material has passed through my hands that the publication of these Studies is resumed with more confidence.

[2] "Notice of a Fossil belonging to the Class Radiaria, found by Dr. Bigsby in Canada": Zool. Journ., vol. ii, pp. 318–20, pl. xi, fig. 5; London, October, 1825.

[3] Mem. Geol. Surv. Gt. Brit., vol. ii, pt. ii, 1848; see pp. 519 and 520.

[4] Rep. Progress Geol. Surv. Canada, 1853–6, p. 292; Toronto, Autumn of 1857.

[5] Op. cit., p. 294.

[6] Canadian Organic Remains, dec. iii, p. 84, pl. viii, figs. 3 and 3*a* (the holotype), 4 and 4*a* (Bigsby's specimen).

Geological Survey, and he kindly made a search which was at last successful. I have to thank him and the then Director General of the Survey for graciously allowing me to retain this specimen from 1897 till the end of 1898. It bears the following labels:—"Agelacrinites Bigsbii / Falls of the Chaudière / Ottawa Rivr. Canada / Pres. by Dr. Bigsby 1848 / E F Δ", "M.P.G.," "6259." The label suggests that Forbes really did fully share the original misapprehension of Billings.

In 1881 a figure described as "Specimen of *Agelacrinites Dicksoni* from the Cabinet of Dr. Grant" was published as fig. 9 of a plate illustrating "Description of a new species of Porocrinus, &c.," by James Grant, M.D., etc. (Trans. Ottawa Field-Nat. Club, No. 2, pp. 42–4). No reference to the specimen was made in the paper or elsewhere in the number.

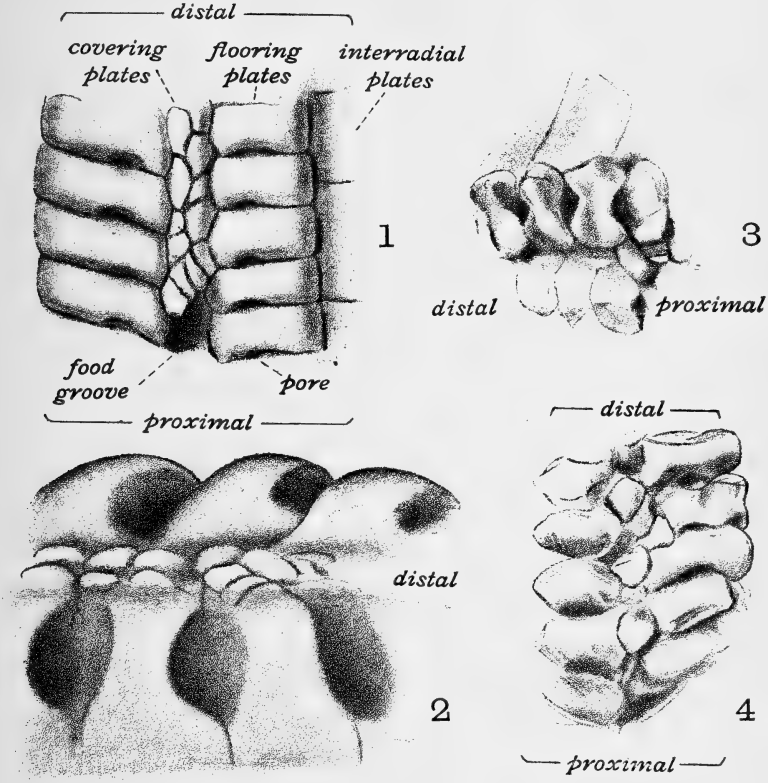
Description of Bigsby's Specimen.

The specimen overhangs the edge of a triangular fragment of limestone, with sides respectively 56, 70, and 76 mm. long. The rock is composed of fragments of coral, monticuliporoids, and pelmatozoa; bits of undeterminable brachiopod shells are visible, but I cannot detect the "single spiral univalve" which Sowerby says "is also to be observed." There is, however, on one side a fragment of some subcylindrical object, with irregular longitudinal striæ on its surface; it is fully 6 mm. long and 2 mm. in diameter. The whole has the characteristic black tint of Trenton Limestone. The upper surface is curiously weathered, and on it lies a fragment, apparently of a *Pleurocystis*, with a part of one of the brachioles. The two echinoderms have the actual test preserved in highly crystalline carbonate of lime coloured by iron rust. The rugose surface of the Edrioasteroid may be due to partial solution and redeposition of calcite; the study, and especially the figuring, of the specimen is thus a task of much difficulty. The under surface of the specimen is obscured by the matrix, even where it overhangs. An attempt to remove some of this has revealed a few doubtful traces of plates. The posterior and right and left posterior interradii are fairly preserved, but the other two are incomplete, and from the left anterior the greater part of the test has been removed.

The periphery is very obtusely pentagonal; as to this I do not share Sowerby's hesitation. The theca rises above the periphery to a height of about 5 mm., which height is attained by the plates of the radial grooves and of the right posterior interradius. The plates in the latter, however, have been raised since death. The above-mentioned traces of plates suggest that the under surface was not flat, and one might hazard a conjecture that the total height of the animal was about 6 mm.; but it may have been excavated around the abactinal pole. The sagittal diameter was about 20·5 mm. The greatest width, measured along the right posterior interradius and left anterior radius, is 23·5 mm. The length of a side is roughly 11·5 mm.

On the Upper Surface the five Subvective Grooves radiate with a sinistral curve, which, to a distance of about 6 mm. from the actinal centre, is hardly perceptible, but then becomes more pronounced.

The grooves reach the periphery, but do not curve round it or pass over it. They would therefore have been invisible from the under surface. The left posterior groove attained a length of 19 mm. from the actinal pole; the left anterior and right posterior were about 1·5 mm. shorter; the others are too imperfect to measure accurately.



SUBVECTIVE SKELETON OF *Lebetodiscus Dicksoni.*

FIG. 1.—Portion of a ray, showing relations of covering-plates to food-groove and flooring-plates; slightly diagrammatised. × 6 diameters.

FIG. 2.—Portion of a ray, seen in three-quarter perspective, showing covering-plates and the excavation of the flooring-plates; slightly diagrammatic. × 20 diam.

FIG. 3.—Portion of the anterior ray, showing how pores are formed by lateral excavation of flooring-plates; sketched under the microscope. × 6 diam.

FIG. 4.—Similar appearances in another part of the same ray, with some covering-plates; sketched under the microscope. × 6 diam.

(All drawings made from Bigsby's specimen.)

The skeleton of the subvective grooves is stout and raised above the general surface to a height of about 1·2 mm. in their proximal regions. The width near their proximal ends is 2·8 mm.; they taper gradually distalwards, and are rounded off rather bluntly. Each is clearly seen

to be composed of a double row of flooring-plates, alternately arranged. These are rounded, and have in places a slight appearance of overlapping by their proximal margins. In the proximal region of a groove, the long axis of any one of these plates is directed almost at a right angle to the median line of the groove, but tends in a distal direction; its length is 1·6 to 2 mm.; the breadth of such a plate is ·9 to 1 mm. There are from 21 to 25 plates along each side of a groove: the lower numbers are on the adjacent sides of the right and left pair. The greatest number is on the adanal side of the left posterior ray.

Each of these plates is excavated on its sides, but more on the side towards the distal end of the ray (Fig. 2), so that the adjacent excavations form a pore, which lies about half-way between the middle line and the outer margin of the whole ray. The actual food-groove was very narrow, and appears to have been covered with irregular plates, some of which are preserved in places (Fig. 1). These covering-plates, though small in proportion to the whole structure, are large compared with the food-groove and do not seem to have had a regular alternating arrangement. As to their existence, I have no doubt; but the state of preservation of the fossil forbids a more accurate account.

The actinal centre is roofed over by relatively large irregular plates, one or two of which are broken away on the right side, so that one gets a suggestion of the underlying hollow, or vestibule of the mouth. These covering-plates appear to be serially homologous with those of the grooves, and their relations to them and to the flooring-plates are best seen in the right posterior ray.

The Interradial Areas are bounded by the flooring-plates of the grooves and by the periphery, but were not separated by any differentiated area from the under surface. They are covered with relatively large and apparently thick plates of irregular shape. The adoral margin of each plate slightly overlaps the adjoining margin of the adjacent plate. This gives the effect of a slight adoral imbrication, more perceptible the nearer the periphery. The plates become a trifle smaller towards the periphery, but there is no sudden diminution of size, and no break in their continuity with the peripheral plates of the under surface. The plates are rugose, but it is hard to determine precisely how far this is due to original ornament. At about halfway between the actinal centre and the periphery the width of the right posterior area is 5·4 mm., that of the posterior area 8·5 mm. The distance from the distal extremity of the left posterior ray to that of the right posterior ray is 15·1 mm., to that of the left anterior is 13·6 mm. The distance between the distal extremities seems to have been a little less than 13·6 mm. in the other interradii, but exact measurements are not obtainable.

The conspicuously greater width of the posterior interradius is due to the presence of the Anal Opening, clearly recognisable as such. Its centre is 6·5 mm. from the actinal centre, and nearly on the middle line of the interradial area. The plates of the valvular pyramid, if they ever existed, have disappeared. The opening which remains is surrounded by a border of plates smaller than the others of the same area, into which they merge, and slightly raised above them, but not

governed by a definite arrangement. The diameter of the opening is about 2 mm.; that of the whole ring is about 4·5 mm.

The Under Surface is so obscured by a hard matrix that one cannot, even after many days labour, be sure of its structure. Fragments seen below the end of the left posterior ray and of the posterior interradius, towards its right side, suggest that there was a pavement of irregular polygonal plates, about 9 to a square millimetre, not imbricating, but probably set in a flexible integument. A broken edge visible in the left anterior interradius, suggests that the larger plates around the periphery formed a stoutish frame, and that the minutely plated central integument stretched loosely across from this frame. Such a suggestion is at least in accordance with the little that we know of this region in the Edrioasteridæ. At the same time there is room for doubt whether all the appearances actually proceed from portions of the individual.

Remarks on the Holotype and on Billings' Description.

The type-specimen of this species is "a fragment, consisting of one perfect ray and two of the interradial spaces," preserved in the Museum of the Geological Survey of Canada, at Ottawa. Since this was the only specimen in the possession of the Survey in 1856, I assume it to be the same as that taken by Billings to London, and figured in Decade iii, pl. viii, figs. 3, *3a*. These figures, however, show two complete rays and considerable portions of three others. Only two interradial areas, however, are at all complete, and neither contained the anus. No central aperture is to be distinguished. The specimen "is quite flat, and appears to have been firmly attached." There is no reason to doubt that Bigsby's specimen, as well as the "other specimens" alluded to by Billings, were rightly referred by him to this species.[1] Moreover, since his second account was actually based largely on Bigsby's specimen, any differences between that account and the description now given must be differences either of observation or interpretation. Let us consider them.

"The diameter . . . is from three-quarters of an inch to an inch and a half." Billings' fig. 4 represents our specimen as $1\frac{1}{16}$ inch along a diameter which is really $\frac{15}{16}$ inch. It is therefore a medium-sized specimen. The type-specimen, as drawn, would have had a diameter of $\frac{19}{32}$ inch, and is therefore a very small specimen.

"The rays . . . are bounded by two rows of small plates, which . . . arch over the grooves. The upper ends of the plates on one side meet those of the opposite side, in a line along the centre of the ray, thus forming for each ray a sort of covered way." In other words, the plates called by me 'flooring-plates' were regarded by Billings as covering-plates, and he did not see the true covering-plates at all, which he was hardly likely to do unless he specially looked for them. But, besides this, the plates in question do not arch over so as to form a covered way, but occupy the full thickness of the ray, as may be seen in section at the end of the anterior ray of Bigsby's specimen.

[1] Should it ever be proved that Bigsby's specimen is of a different species, it will have to receive a new name; and that new species must then be taken as the genotype of *Lebetodiscus*.

"In all the specimens . . . the rays curve round to the right hand." As the figures show, this means sinistrally or contra-solar, as is actually the case in Bigsby's specimen.

"The marginal plates of the rays do not appear to alternate regularly." They do alternate, however, and the contrary appearance is due to the irregularities of the covering-plates.

"There are two rows of small circular indentations on each side of the rays, corresponding in their position to the ambulacral pores of *E. Bigsbyi*, only that in the latter they are in the bottoms of the grooves." I only see one row of 'indentations,' but the appearance of another row is occasionally produced on the extreme edge of the ray by the rounding of the ends of the flooring-plates. The structure of the anterior ray in our specimen leaves me in no doubt that the indentations were actual pores, corresponding to the pores of *E. Bigsbyi*, which had only one row of pores, not two, as Billings supposed.[1] The difference between the two forms really is that here the pores are well outside the covering-plates, whereas in *Edrioaster* they were roofed in by them, a fact not known to Billings.

Remarks on other Specimens referred to *A. Dicksoni.*

The specimen formerly belonging to Dr. James Grant has already been mentioned. Since the present paper was first written, Dr. J. M. Clarke, in a valuable article entitled "New Agelacrinites" (Bull. N.Y. State Mus., vol. xlix, pp. 182–98, pl. x, December, 1901), has published a diagram based on Grant's figure (p. 190, fig. 3), and from his legend it appears that the diameter of the specimen is only 21·5 mm., and not 48 mm. as it appears in the original drawing. These illustrations indicate some resemblance to Bigsby's specimen, but the small adorally imbricating plates seen on the margin in the right anterior interradius do not appear in harmony with the adjoining plates of the periphery, which are all large, just as they are in Bigsby's specimen. At all events, such a figure, unsubstantiated by any description, cannot be held to prove the existence of the imbricate border characterising *Agelacrinus*, *Lepidodiscus*, and a few other genera.

A distinct imbricate border of *Agelacrinus*-type is shown in pl. ii, fig. 2, of Professor Otto Jaekel's "Stammesgeschichte der Pelmatozoen" (Berlin, 1899). The specimen, which is in the collection of Professor Frech at Breslau, and comes from the Trenton Limestone of Ottawa, is assigned by Dr. Jaekel to *A. Dicksoni*. On p. 50 he says of this species: "Thecalplatten zwischen den Ambulacren besonders gross, Ambulacra ziemlich kurz gedreht, Saumplättchen stark skulpturirt." The word 'Saumplättchen' is usually translated by 'covering-plates' or 'ambulacrals,' and in the explanation to pl. ii Dr. Jaekel applies the word 'Ambulacralia' to two of the plates that in his opinion cover the subvective groove. These are strongly pitted on the sides

[1] See the diagrams and brief account of *Edrioaster Bigsbyi* in "A Treatise on Zoology," ed. E. Ray Lankester, vol. iii, Echinoderma, p. 209. Also F. A. Bather, "What is an Echinoderm?" 1901, and Encycl. Brit. Suppl., Art. Echinodermata, 1902.

(perhaps for the reception of smaller plates), but do not appear to be of the same character as either the flooring-plates or the covering-plates in Bigsby's specimen of *A. Dicksoni.* It is, in fact, clear that the specimen figured by Dr. Jaekel differs in its peripheral zone and in its subvective skeleton from our species, and that in those points it has the character of an ordinary *Agelacrinus.*

With the language used by Dr. Jaekel it is not easy to reconcile the following sentences in Dr. Clarke's paper (op. cit., p. 191):—"Billings claimed that in the Trenton species *A. dicksoni*, perforated ambulacral plates were exposed, but this observation has not been confirmed and Jaekel holds that no ambulacral plates were present in these bodies. At all events usually only the cover plates have been observed." I am not sure what this means, but it is certain that the plates between which Billings described 'indentations' were those here called flooring-plates, and it is highly probable that these indentations were podial pores. It is also certain that these same plates were identified by both Billings and Jaekel with the 'covering-plates' or 'ambulacrals' of a crinoid arm, and that they did not mention the smaller covering-plates, which, in my opinion, are the only homologues of crinoid 'Saumplättchen.'

Of recent years the only other reference to the species has been the record of its occurrence in Trenton Limestone at Pakenham, Ontario, by Dr. H. M. Ami (Ann. Rep. Geol. Surv. Canada, xiv, p. 84 J; January, 1905).

Systematic Relations of the Species.

There still are problems to solve with regard to *Agelacrinites Dicksoni*; but there are problems presented by the majority of Edrioasteroidea, and we certainly know enough to make comparison with other forms profitable.

Taking the families of Edrioasteroidea as defined in Lankester's "Treatise on Zoology" (vol. iii, pp. 207–9, 1900), we may at once set aside the Cyathocystidæ with their massive theca, and the Steganoblastidæ with their stem.

Turning to the Agelacrinidæ, with which the species has always been placed, we see that from *Stromatocystis* it is separated by the imbrication of the interradial plates and the curvature of the rays. The latter feature also distinguishes it from *Cystaster* and *Hemicystis.* It is further separated from *Cystaster* by the large size of its interradials, and from *Hemicystis*, *Agelacrinus*, *Streptaster*, and *Lepidodiscus* by the absence of the differentiated marginal zone, which in those forms is always obvious and often highly differentiated. I also incline to regard it as having had a less flattened and less sessile habit than the genera just mentioned. Similar features, as well as the clear alternation of the flooring-plates of the grooves, enable us to discriminate between it and the little-known *Haplocystis* of Roemer. As for the Carboniferous form to which in 1897 Gregory gave the name *Discocystis*, we know, at all events, that it had no imbricating plates, and that the margin was more distinct than in *A. Dicksoni.*

A more important character than any of those mentioned is presented by the structure of the subvective skeleton. It seems

clear that the side-plates, here called flooring-plates, are homologous with the flooring-plates of *Edrioaster*. Whether those plates have homologues in the Agelacrinidæ is matter for debate; at any rate, no genus of that family has similar plates with intervening depressions so like pores. The covering-plates also seem homologous with the covering-plates of *Edrioaster*, and it is doubtful whether the so-called 'ambulacrals' of the Agelacrinidæ are of the same nature; if they are, they have, at any rate, different relations to the adjoining plates.

Proceeding then to compare the species with other Edrioasteridæ, we note that it differs from them in the restriction of the grooves to the actinal surface, in the small size of the covering-plates, and in the absence or very slight development of an abactinal frame.

The species therefore appears to represent a generic type hitherto unrecognised, and a type of considerable interest in that it is intermediate in so many features between Edrioasteridæ and Agelacrinidæ. What bearing this may have on the classification of the Edrioasteroidea must be reserved for discussion after more of these Studies shall have been published. For the present, the following diagnosis may be offered.

Lebetodiscus[1] gen. nov.

An Edrioasteroid, with theca flattened below, convex above; no marginal zone on actinal surface; no definite abactinal frame; interradial thecal plates relatively large, with slight adoral imbrication; rays curved [contra-solar in genotype], and reaching but not passing the periphery; subvective skeleton of alternating flooring-plates, with intervening pores, and small irregular covering-plates.

Genotype: *Lebetodiscus Dicksoni* (E. Billings, sub *Agelacrinites*).[2] Lower Trenton Limestone, Ottawa.

It may be worth noting that a restored representation of the fossil herein described, by J. S. and A. B. Wyon, adorns the reverse of the Medal founded in 1887 by Dr. Bigsby and awarded biennially by the Council of the Geological Society of London. To judge from the illustration facing p. 252 of Mr. Horace Woodward's "History" of the Society (1907), the medal gives a good general idea of *Lebetodiscus Dicksoni*.

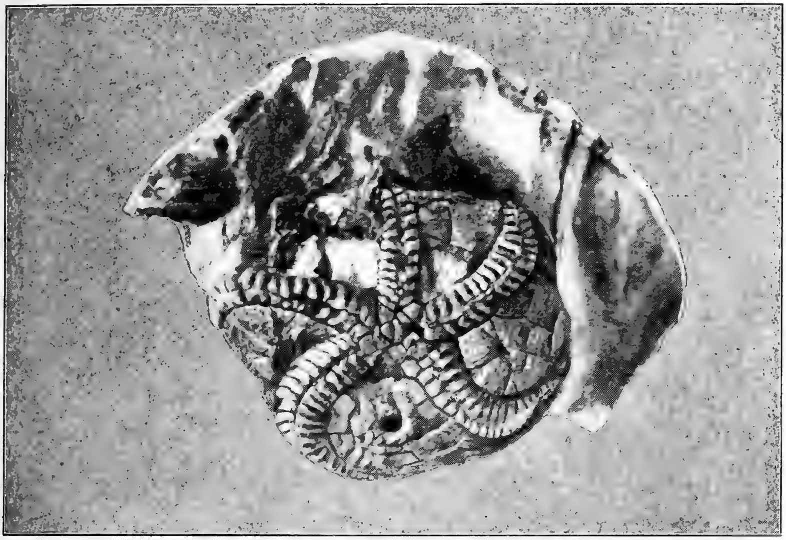
EXPLANATION OF PLATE XXV.

The Upper Figure is taken from a photograph of Bigsby's specimen of *Agelacrinites Dicksoni* Billings, the type of *Lebetodiscus*, enlarged two diameters. Only a part of the matrix is shown. The posterior interradius, with the anus, is towards the observer.

The Lower Figure represents the Lower Trenton Limestone of Table Rock at Chaudière Falls, Ottawa River, where Bigsby collected the specimen figured above.

[1] *Lĕbētodiscus*, from λέβης, a cauldron; after the Chaudière Falls; and δίσκος, a round plate.

[2] But see footnote 1, *ante*, p. 547.



LEBETODISCUS.

IV. The Edrioasters of the Trenton Limestone.[1]

[Part I.]

[Geol. Mag., n.s., Dec. VI, Vol. I, pp. 115–125, Pls. X, XI, XII; March, 1914.]

Previous History.

EDRIOASTER bigsbyi was first made known by E. Billings in June, 1854,[3] and was referred by him, though with some doubt, to *Agelacrinites*. He gave no specific name, but regarded his fossils as identical with the specimen found by Bigsby at the Chaudière Falls and described by G. B. Sowerby in 1825 (see Study III), and as "almost identical with *A. Buchianus*" of Forbes, 1848 (see Study II). This series of papers by Billings contains several important observations and reasonings not reproduced in those later more official publications of his to which alone subsequent writers seem to have gone for information. From the original account it is clear that the specimens there called *Agelacrinites* were the same as those which Billings described in 1857, under the name *Cyclaster bigsbyi*.[4] The misapprehension that caused Billings to apply to his new species the trivial name *bigsbyi* has already been dealt with in Study III; the species has nothing to do with the specimen found by Bigsby. In 1858 Billings discovered and pointed out his error, and, realizing further that the generic name *Cyclaster* had been taken by G. Cotteau for a sea-urchin a few months before his own use of it, he redescribed the species under the name *Edrioaster bigsbyi*.[5] The independence of the genus itself was denied in 1860 by E. J. Chapman, who referred the species back to *Agelacrinites*.[6] The textbook writers, however, generally accepted *Edrioaster*, and no change was made in either name or description until Professor Haeckel in 1896 thought fit to alter the name to *Edriocystis*.[7] Neither the nomenclatoral nor the taxonomic vagaries of Professor Haeckel won any favour, and it is needless to allude further to him or to other writers who shared his ignorance of the facts but not his imagination. In that category I do not include Professor O. Jaekel, but even he, in his *Stammesgeschichte der Pelmatozoen* (1899, p. 46), contented himself with the information and figures published by Billings in 1858, apart from such hints as he could glean from the manuscript of my then forthcoming Study II.

[1] Plates X and XI of the present Study were drawn in 1900, and diagrams made from the specimen represented in Plate X have been published by me in 1900, 1901, 1902, and 1911. The completion of the present paper has unfortunately been delayed by the pressure of official duties and other scientific work.

[3] Canad. Journ., vol. ii, pp. 271–4, figs. 10–12.

[4] Rep. Progress Geol. Surv. Canada, 1853–6, p. 293, Toronto, autumn of 1857.

[5] Canad. Org. Rem., dec. III, p. 82, pl. viii, figs. 1, 1*a*, 2, 2*a*, June, 1858.

[6] Canad. Journ., n.s., vol. v, p. 364.

[7] "Amphorideen und Cystideen," pp. 117–8, Festschr. f. Gegenbaur, 1896.

In brief, then, from the time of Billings down to the end of last century, the genus *Edrioaster* remained most imperfectly, not to say incorrectly, apprehended. Its importance was obvious, but I did not dare to introduce it into any system of classification or any theoretical discussion without having first-hand knowledge. The opportunity for obtaining this was afforded by my friends Mr. Walter R. Billings, of Ottawa, and the late J. F. Whiteaves, of the Canadian Geological Survey, who lent me excellent material, which I was fortunately allowed to retain for several years. The need of time as well as of material has never been more obvious. Before any precise account could be written or any adequate figure drawn, it was necessary to clean and develop the specimens with the utmost patience. And here I have to acknowledge the great help rendered by my wife, who devoted months of labour to a single specimen, thus enabling Mr. G. C. Chubb to make the admirable drawings on Plate X. The information thus obtained was utilized in the diagrams and brief account of *Edrioaster bigsbyi* published in *A Treatise on Zoology*, vol. iii, Echinoderma, p. 209 (London, 1900), in the abstract of a lecture "What is an Echinoderm?" [1] and in the *Encyclopædia Britannica* articles on "Echinodermata" (1902) and "Echinoderma" (February, 1911). That specimen has been still further cleaned, several other specimens have been prepared and studied, and the results are given in the present paper.

Since 1900 the only author to pay any particular attention to my publications on Edrioasteroidea has been Mr. W. K. Spencer, who criticized some of my conclusions in his interesting paper "On the Structure and Affinities of *Palæodiscus* and *Agelacrinus*" (Proc. Roy. Soc., vol. lxxiv, pp. 31–46, pl. i, 1904), but who has since modified his objections ("Brit. Palæoz. Asterozoa": Palæont. Soc. vol. for 1913).

Material.

The holotype of *Edrioaster bigsbyi* has never yet been fixed, and should be chosen from among the original specimens described and named by E. Billings (1857). On the generally admitted assumption that these comprised the original of Billings' pl. viii, fig. 1 (1858), I hereby select that specimen as holotype. This and the other specimens described and figured by Billings in 1857 and 1858 are kept in the Victoria Memorial Museum at Ottawa. These specimens are so imperfectly preserved that Mr. Whiteaves did not consider it worth while to send them to me. He sent, however, the following three specimens, the property of the same museum, and belonging without any doubt to the same species. For convenience of reference I have lettered them A–C.

A. The original of Plate X. A theca in calcite in a matrix of very hard, grey, shaly limestone, which, when the specimen was sent me, covered the whole of its underface, but is now cleaned away. The specimen is broken into three parts by a crack across the anterior ray and another across the distal end of the right anterior ray. Part of the theca comprising the distal end of the anterior ray is missing.

[1] Journ. London Coll. Sci. Soc., vol. viii, pp. 21–33, May, 1901. Also *Che cosa è un Echinoderma?* Torino, October, 1901.

B. The original of Plate XI. A theca lying on a small block of hard, black, shaly limestone, so that only the upper face is exposed. This retains the cover-plates, which, however, are crushed in.

C. The original of Plate XIII. A theca of which the upper or oral face is covered with yellowish matrix, but of which the under or adapical face has been well exposed.

In the absence of detailed information, it is assumed that these specimens came from the neighbourhood of Ottawa, as did all those mentioned by E. Billings.

Mr. Walter R. Billings lent me the following specimens of the genus, and ultimately with singular generosity presented them to the British Museum, under whose register numbers they are here quoted.

E 16173, a medium-sized specimen, with radius *ca.* 18·5 mm. Adoral face disturbed and weathered, with hard black shale in the hollows. Adapical face worn, and obscured in centre by hard limestone matrix. Collected by W. R. Billings at Belleville, Ont., on right bank of the Moira, a quarter of a mile above the railway bridge (*E. levis*).

E 16172, a smaller specimen, with radius *ca.* 16 mm. Most of the right side is missing; rest of adoral face fairly preserved. Adapical face partly obscured by limestone and grey shale, since removed. Collected by W. R. Billings at Peterborough, Ont. (Pl. XIV, Figs. 2, 3.)

The British Museum has still more recently acquired—

E 15930, a rather large individual, radius *ca.* 25 mm., poorly preserved. Adoral face much rubbed. Adapical face coated with hard black shale, now removed. From Mount Sherwood, a suburb of Ottawa. W. R. Smith Collection, 1909. (Pl. XIV, Fig. 1.)

E 16054, a smaller individual, radius *ca.* 11 mm., preserved obliquely and therefore less flattened, in a brown, sandy, calcareous shale. From Belleville, Ont. W. R. Smith Collection, 1909.

E 15900, a rather large individual, radius *ca.* 23 mm. Adoral face fairly well preserved. Part of the adapical face exposed. Matrix a dark-grey shale. From Kirkfield, Ont. Presented by Professor W. A. Parks, 1909. (*E. levis*, Plate XII.)

Horizon.

All the known specimens are from the Trenton Limestone.

In the absence of more precise information, I take the horizon at Ottawa to be probably the limestone with shale partings which Dr. P. E. Raymond (1912[1]) assigns to his Horizon 5; but it is also possible that some specimens are from his lower Horizon 2, which is exposed in the Hull quarries. E. Billings (1854, p. 272) found "seven specimens . . . within a space of four square yards in extent, and partially embedded in the surface of a stratum of limestone. Along with them were" trilobites, crinoids, *Amygdalocystis tenuistriatus*, and a quantity of *Chætetes lycoperdon*. These, with others, were all "in the upper one hundred feet of the Trenton limestone" (p. 273).

[1] 1912, Summary, Rep. Geol. Surv. Canada, 1911, p. 354.

Specimen E 15900 from Kirkfield is probably from Horizon 2, which is well developed at that place.

I have no external evidence as to the horizon of the specimens from near Belleville, or of that from Peterborough.

E. bigsbyi has also been recorded from the *Fusispira* and *Nematopora* beds, in the middle of the Trenton group, in Minnesota (N. H. Winchell & E. O. Ulrich, Final Rep. Geol. Surv. Minnesota, vol. iii, pt. ii, p. cxxiii, 1897).

General Description.

The theca has an approximately circular periphery, and a diameter varying between 20 and 50 mm. As in *Dinocystis barroisi* (Study I) and *Edrioaster buchianus* (Study II), the general shape is that of a Tam-o'-Shanter cap or a Breton béret (Text-fig. 1).

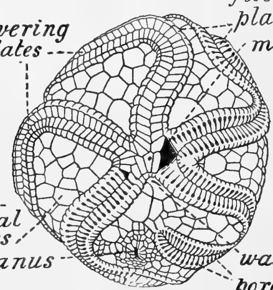


Fig. 1. *Edrioaster bigsbyi.* The adoral face, slightly restored from specimen A. The cover-plates are removed from rays I, IV, and V, but remain on rays II and III. Natural size.

The mouth is at or near the centre of the convex face, and from it five subvective grooves pass over the theca on to the concave face. Each groove is sharply curved as it approaches the periphery; the curve of the right posterior is probably always solar (= dextral), that of the others is contrasolar in the type-species. Each groove is floored by an alternating series of plates (floor-plates), and roofed by alternating movable cover-plates, one to each floor-plate. The median line of each groove is depressed to form a channel, from which branches are given off to right and left between the floor-plates. Each branch ends at a pore, which passes down the suture between the adjacent floor-plates into the thecal cavity. These pores are close to the margins of the groove, but beneath the cover-plates.

The mouth opening (peristome) is surrounded by skeletal elements continuous with the floor-plates, and is roofed by plates continuous with the cover-plates.

The thecal plates of the convex face between the rays (interradials or interambulacrals) are relatively large, irregular in shape and size, and do not imbricate.

In the posterior interradius, two large interradials, adjoining the peristome, are traversed by an elongate hydropore.

In the same interradius lies the anal opening (periproct), surrounded by smaller interradials.

On the concave face are seen the end of the rays, stiffening the periphery. Within them are some irregular plates continuous with the interradials; and then a circular frame of rather larger and stouter plates. Loosely stretched across the space within this frame was a flexible integument, filled with minute plates. This integument was generally protruded round the centre in roughly U-shaped lobes, apparently five in all, but often irregular, at least in the fossils.

Detailed Description.

This is based mainly on specimen A, but measurements and occasional details are also given on the evidence of the other specimens. It will soon be manifest that specimens E 16173 and E 15900 represent a species distinct from *E. bigsbyi*, to which all the other specimens appear to belong. For this new species the name *E. levis* is proposed.

The Periphery is roughly circular, with irregular swellings and indentations formed by the rays, and varying in position according to the curvature of the rays. The circular form is sometimes further departed from, in consequence of either natural growth or post-mortem pressure, as appears from the following measurements in millimetres:—

	A	B	C	E 15900	E 16173
Sagittal diameter . .	36·2	43·5	*ca.* 37	*ca.* 40	36
Transverse diameter . .	34·5	46·4	*ca.* 37	*ca.* 40	35·6

From the periphery, the theca rises steeply at first, but soon bends adorally in a low arch; towards the adapical face it bends rapidly downwards and inwards, and turns upwards as soon as the rays are passed. When specimen A is placed on a flat surface the theca reaches a height of 11·5 mm., exactly one-third of its transverse diameter. The adapical face is excavate to about 6·5 mm., so that the length of the polar axis is about 5 mm. The specimen does not appear to have undergone more compression along this axis than it may have been capable of effecting spontaneously during life. It is, however, probable that in life the adapical integument hung lower than it is found in the fossil, so that the height of the excavation would have been about half the total height of the theca under normal conditions. The other specimens are not so preserved as to lend themselves to exact measurements in these respects; but, broadly speaking, the larger the theca the more relatively flattened does it appear. This may be due to subsequent pressure in the plane of bedding. Contrariwise, E 16054, which exceptionally lay oblique to the bedding plane, has had its relative height exaggerated by compression. E. Billings' pl. viii, fig. 1*a* (1858) shows a section across a partly crushed specimen. If this be restored to its probable original shape, the measurements are approximately: thecal diameter, 59 mm.; thecal height, 22 mm.; height of adapical excavation, 13 mm. This is one sixth larger than any actual specimen I have seen.

Specimens that have clearly been flattened in one or another plane show some displacement of the thecal plates, and this fact, taken together with the solidity of all thecal elements other than the apical

integument, shows that the theca as a whole was not particularly flexible.

On the Adoral or Upper Face are the five Radial Grooves, of which the course may first be traced in specimen A (Pl. X, Fig. 1). All proceed with a very slight curve to a distance of about 15 mm. from the oral pole. The antero-lateral and postero-lateral rays have the concave side of this curve turned towards the postero-lateral interradii; in other words the rays of the right-hand pair and of the left-hand pair respectively bend towards each other. In the anterior ray the concavity faces the right. That is to say, the proximal curve of the left posterior, anterior, and right anterior rays (I, III, IV) is solar or dextral, and that of the left anterior and right posterior rays (II, V) is contrasolar or sinistral. All the rays except the right posterior then suddenly bend in a contrasolar direction, and after bordering the periphery for the space of an interradius, pass on to the under surface of the theca, where they continue in the same direction for the further space of an interradius, ending near the adjacent ray (Pl. X, Fig. 3). The only exception to this regularity of these four rays is that the peripheral tract of the right anterior ray bends upwards for a short distance within the right anterior interradius (Pl. X, Fig. 1). The right posterior ray, however, bends in a solar direction, and returns on the posterior interradius, ending on the oral face at a point a little to the right of the periproct, and about 9·5 mm. from the oral pole (Pl. X, Fig. 1). In consequence of this, the peripheral tract of the left posterior ray passes across both the posterior and the right posterior interradii, and ends against the right anterior groove (Pl. X, Fig. 2).

The varying curves of the rays in this specimen A and their sharp definition give them a peculiar aspect of independent life. The width of a ray in the proximal half of its course is 5·5 mm., or slightly less when close to the peristome; where it bends, the width is 4·5 mm.; on the under side it gradually tapers to 3 mm., after which it is rapidly rounded off.

In specimen B the general shape and disposition of the rays is precisely as in A, except that the anterior ray does not begin with a solar curve, but runs straight to the main contrasolar flexure. The width of a groove in the proximal half is about 6·3 mm., but may be reduced to as little as 5·5 mm. at the bend (Plate XI).

In specimen C the adoral region is covered with matrix, but from the marginal tracts it can be inferred that the general disposition of the rays is as in A and B (Plate XIII).

Specimen E 16172, so far as preserved, indicates a similar arrangement.

In E 15930 the proximal curve of the rays is contrasolar in the left posterior, left anterior, and right posterior (I, II, V), and solar in the other two rays. The distal curve of the left posterior, left anterior, and right anterior rays is visible on the under side of the theca and is contrasolar (Plate XIV). Probably the general arrangement was as in A.

E 16054 is a young individual, as shown not merely by its small size, but by the small extent of the periphery occupied by the distal

tracts of the rays, which do not stretch half-way across the interambulacrum. Owing to lateral compression, the curves are not very clearly seen. The proximal curve is solar in the right anterior, contrasolar in the right posterior ray, as in A. The distal bend is clearly contrasolar in the left anterior ray, and appears to have been the same in the others, except in the right posterior, where it is solar but cannot be traced far.

The rays in E 16054 are not only relatively shorter, but taper more rapidly than in older individuals. Thus the left anterior ray is 4·1 mm. wide in the extreme proximal region; 3·1 mm. wide at about half-way to the periphery; 2·4 mm. at the periphery, whence it rather quickly rounds off.

Specimens E 15900 and E 16173 (*E. levis*) differ conspicuously from the others in that the main distal curve is solar in all rays, and that the right posterior ray, instead of being recurved, passes along the periphery of the posterior interradius and bends round like the other rays to end on the adapical face. In E 15900 the proximal curve is solar in all rays except the left anterior (II) ray, where it is contrasolar (Plate XII). In E 16173 the proximal tract is not clearly seen in ray II; in all others the curve is solar.

Summing up the evidence before me as to the distal curvature of the rays, it appears that in all individuals that of the right posterior ray, when known, is solar, that in six individuals (A, B, C, E 15930, E 16054, and E 16172) that of all the other known rays is contrasolar, and that in two individuals (E 15900 and E 16173) it is solar. Billings (1858), pl. viii, fig, 2, also represents two rays with a contrasolar bend. Although Billings (1858, p. 83) says that the rays curve "towards the right in some specimens, and towards the left in others", I know of no evidence for a contrasolar bend of the right posterior ray, and seeing that it is solar in all of our six specimens in which the other rays are contrasolar, it is hardly likely to have been contrasolar in any other case. Neither do I find evidence for any individual ray or rays (the right posterior always excepted) bending in a direction contrary to the majority, as does the right anterior in the holotype of *Agelacrinus hamiltonensis*.

In his original account (1854, p. 272) E. Billings said that he had found seven specimens, and that in one only did "the rays turn to the right [solar] instead of the left [contrasolar]". It is therefore curious that in his "partly restored figure" 10 (p. 271) he should have represented all the rays as equably solar. This must have been a pure mistake, for Mr. Walter Billings, who kindly looked up this point for me in April, 1900, said that all the ten imperfect specimens then in the museum at Ottawa showed a contrasolar flexure. The one exception mentioned by E. Billings, further distinguished as showing the adapical face, could not then be found. Subsequently specimen C, with the adapical face exposed, turned up in that museum and was sent to me. In it the rays, though contrasolar, appear solar because seen only from the under face. This may have been the specimen referred to by E. Billings, in which case none of the Ottawa specimens would have the rays solar.

The only certain exceptions to the normal arrangement are E 15900 and E 16173, which have the rays all solar; but these, on account of yet other features, are to be separated as a distinct species, *Edrioaster levis.*

The conclusion, then, is that in *Edrioaster bigsbyi* the bend of the right posterior ray is solar and recurved on the interambulacrum, that of all the others contrasolar. In *E. levis* the bend of all rays is solar, and none is recurved. In *E. buchianus* the rays of the only known specimen have the same arrangement. The same is apparently the case in *E. saratogensis* Ruedemann, 1912. For although Dr. Ruedemann says that one of the rays (inferentially the left posterior) is contrasolar, this is borne out only by his own restoration of a specimen in which that ray is not preserved (pl. iii, fig. 3). In his fig. 2 the proximal tract of the right anterior ray has a slight contrasolar curve; but all other rays in all figures are solar or straight in that region. In *Dinocystis barroisi* and in the holotype of *Lebetodiscus dicksoni* all rays are contrasolar. The facts are summarized in the annexed table.

	Proximal.					Distal.				
	I.	II.	III.	IV.	V.	I.	II.	III.	IV.	V.
Edrioaster bigsbyi A . .	S	C	S	S	C	C	C	C	C	S
,, ,, B . .	S	C	R	S	C	C	C	C	C	S
,, ,, C . .	?	?	?	?	?	C	C	C	C	S
E 15930	C	C	S	S	C	C	C	C	C	S
E 16054	?	?	?	S	C	C	C	C	C	S
E 16172						C	C	C	C	S
E. levis—										
E 15900	S	C	S	S	S	S	S	S	S	S
E 16173	S	?	S	S	S	S	S	S	S	S
E. buchianus	R	R	S	S	S	S	S	S	S	S
E. saratogensis . . .	S	S	R,S	S,C	S	S	S	S	S	S
Lebetodiscus dicksoni .	C	C	R	C	C	C	C	C	C	C
Dinocystis barroisi . .	C	C	C	C	C	C	C	C	C	C

S = solar; C = contrasolar; R = straight.

Floor-plates.—The main description applies to *E. bigsbyi*, especially to specimen A; the peculiarities of *E. levis* are noted later.

For the whole of their length the radial grooves are floored by a double series of alternating plates, which meet in a zigzag median suture. These floor-plates are elongate at right angles to the median line of the groove, the width of each plate being less than one-third (*ca.* ·28) of its length. Their outer margins are convexly curved; their abutting margins are straight (Pl. X, Fig. 4). The plates rise

sharply up from the interradial areas, they form a rounded margin on each side of the groove, and then dip almost straight down to the median suture, where they meet at an angle of about 130° (Pl. X, Fig. 6). Near the peristome this angle is slightly less, that is to say the depression is more marked; but at the distal ends it becomes wider and almost disappears. Where the grooves bend sharply, the dip of the floor-plates on the inner side of the curve becomes steeper, and the angle therefore less. All these changes can be traced in Pl. X, Figs. 1–3.

The suture between two floor-plates of the same side of the groove is depressed from a point just within the rounded margin right down to the median suture. The depression is deepest at its outer end, where also it is slightly expanded in circular form; but thence it gradually widens towards the median suture. That suture also is depressed, so that there is a sinuous median channel (Pl. X, Figs. 4, 5).

Further details of structure in the floor-plates are to be noted. The rise above the general surface of the interradial area may be strongly marked; in B it amounts to *circa* 1·9 mm., and about half-way up this outer part of the plate is a slight depression, which seems to continue the pustular ornament of the interradials.

In the proximal half of a groove, in A, the length of each floor-plate (at right angles to the radius) is about 2·7 mm., and the width (measured parallel to the radius) ·75 mm. In B the latter measurement is as much as 1·14 mm.; but as the groove narrows distally this also decreases, so that in the distal part of the right posterior ray it is noted as ·66 mm. At the extreme distal end of a ray, as seen in A, the floor-plates diminish considerably in size, but continue to alternate, and are arranged fanwise. There is no distinct terminal (Text-fig. 4). These appearances were not clearly exposed when Plate X was drawn.

The groove along the suture between adjacent floor-plates was not really so simple as it appears in most specimens. In the left anterior ray of E 16172 (Pl. XIV, Fig. 3) are seen two slight ridges starting from near the centre of the circular expansion (pore), and diverging as they pass, one on each side of the suture. On the side of each ridge remote from this suture are about three slight swellings, and the ridge itself may thus be broken up into a row of tubercles. Round the circular expansion is a slightly raised rim. These features, when once appreciated, can also be detected in parts of specimen A.

In specimens that have not been thoroughly cleaned, the outer circular ends of the depressions between the floor-plates are filled with matrix, and this, according to its amount, gives the appearance of a series of pores or slits. If the matrix be also retained between the divergent ridges just described, it may produce the appearance that in 1858 (pl. viii, fig. 2*a*) misled E. Billings into the supposition that there was a second inner series of pores. Careful removal of the matrix entirely does away with the latter appearance, and reduces the supposed outer series of pores to little more than pin-pricks, each in the centre of the circular expansion (Pl. X, Fig. 4). It has in fact been suggested that further cleaning would do away with the

appearances altogether, and that pores do not really exist (e.g. Jaekel, 1899, p. 21). The presence of pores, however, is proved by the more direct evidence of sections fortunately provided by the cracks across specimen A. One of these cracks (Pl. X, Fig. 1) passes right through a supposed pore on the left side of the anterior ray; removing the loose portion and examining the fractured surface, one sees the dark stain of the pore passing right through the test to the dark impure limestone that fills the thecal cavity (Pl. X, Fig. 6). This section also shows the oblique suture between the floor-plate and the adjacent interradial, sloping from the exterior inwards towards the perradius; and the pore-canal is seen to have a similar obliquity. A like appearance is seen at the distal fractured end of the right anterior ray, which underlies the broken end of the anterior ray; also at the crack that traverses the same ray at right angles to the main crack.

These pores differ from the so-called pores of the Cystidea in two respects: they pass into the thecal cavity; they do not pierce the substance of the floor-plates, but lie in the suture between them. Just as the depression of that suture on the floor of the radial groove forms a channel leading to the peripodium or circular rim round the pore, so on the interior of the test the suture between the floor-plates is depressed as it nears the outer margin of the ray, and thus the pore-canal opens into an elongate depression, as well seen in a part of the right anterior ray of specimen E 16172 (Pl. XIV, Fig. 2). These depressions are the more conspicuous because the general inner surface of the floor-plates is flush with the inner surface of the interradials. These interior openings of the pores were noted by E. Billings in 1854 (p. 272).

It is clear that the appearances in the stereom of the floor-plates, as just described, form the precise counterpart of the appearances in the matrix and internal casts of *Edrioaster buchianus* as drawn and interpreted in Study II (Geol. Mag., 1900, p. 196, Text-fig. 3). What all these appearances may mean will be discussed later, but the objective reality of the pores in *Edrioaster* will, I trust, no longer be called in question.

Certain other markings near the outer margin of the radial groove will be described in connexion with the cover-plates, to which we now pass, leaving the circumoral modifications of the floor-plates for future consideration.

PLATE X.

Edrioaster bigsbyi. Specimen A, from drawings made in 1899 by Mr. Gilbert C. Chubb.

Fig. 1. Adoral face. Towards the observer is the posterior interradius, in which are seen the anus and the hydropore. The dark triangular depression between those structures is due to fracture of the plates. × 2 diam.

Fig. 2. Posterior view. × 2 diam.

Fig. 3. Adapical face, the posterior interradius being away from the observer. × 2 diam.

Fig. 4. Some of the floor-plates, showing the groove that leads from the poral depression to the main radial channel. The depression for the cover-plates is not clear in this lighting. × 10 diam.

Fig. 5. A solid section across the food-groove to show the relation of cover-plates to floor-plates ; based mainly on portions of l. ant. and l. post. rays. × 5 diam.

Fig. 6. A transection of the floor-plates, showing their relation to the interradials. The floor-plate on the left is viewed on its sutural surface, which bears the pore-canal. Based on the broken regions of ant. and r. ant. rays. × 5 diam.

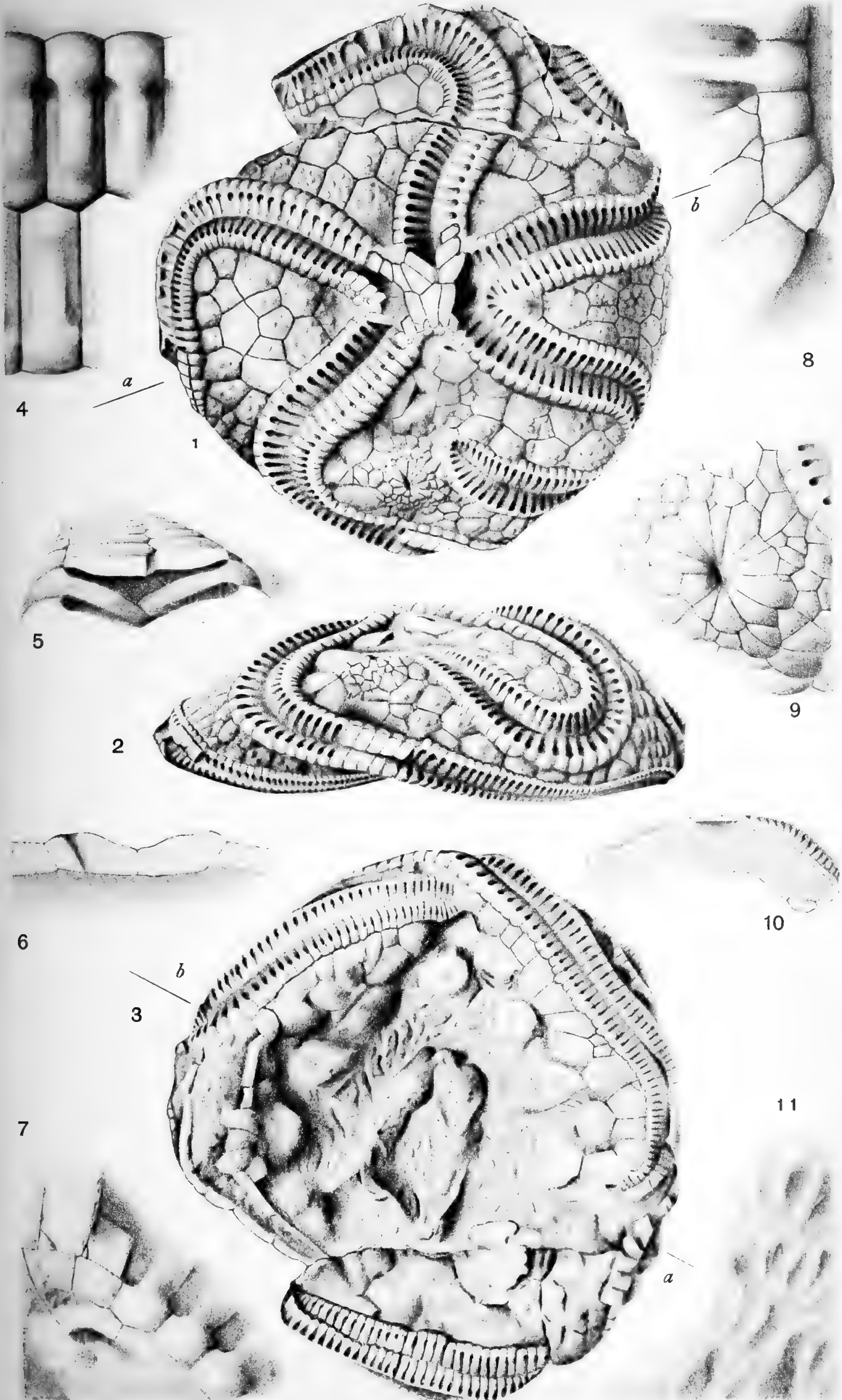
Fig. 7. The hydropore. The adjacent regions of the floor-plates show the depression that receives the ends of the cover plates. × 10 diam.

Fig. 8. Parts of the floor-plates and cover-plates near the peristome, showing the accessory plates. × 10 diam.

Fig. 9. The periproct. × 8 diam.

Fig. 10. A section reconstructed along the line *a–b* in Figs. 1 and 3, showing the approximate thickness of the plates and the relations of the adapical hollow and lobes. Nat. size.

Fig. 11. Part of the thin, plated integument of the adapical face. The actual plates are not so clearly seen in this specimen as they are in some others (cf. Plate XIV). × 20 diam.



G. C. Chubb ad. nat. del. London Stereoscopic Co.

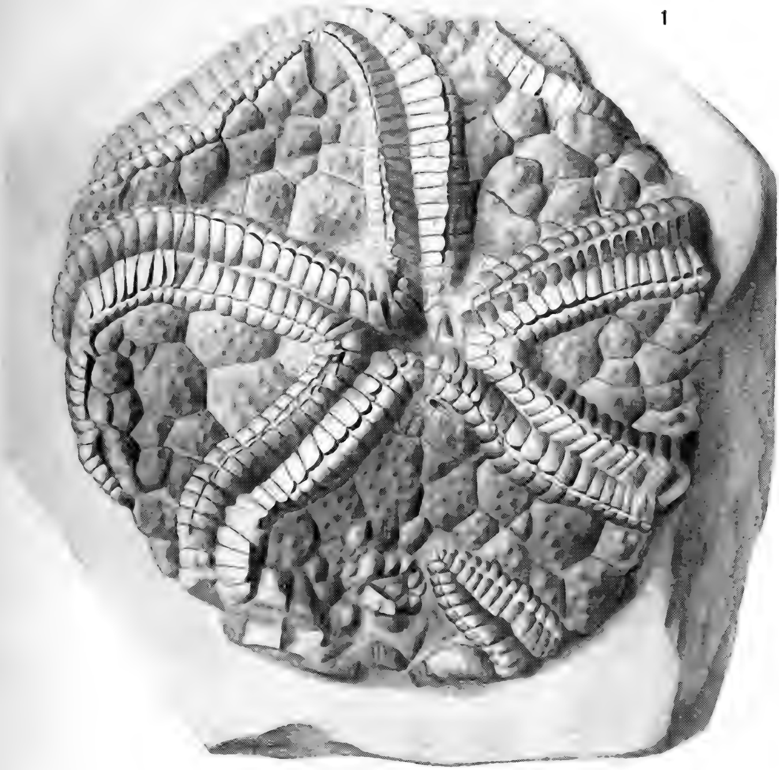
EDRIOASTER BIGSBYI

Plate XI.

Edrioaster bigsbyi. Specimen B, from drawings made in 1899 by Mr. Gilbert C. Chubb.

Fig. 1. Adoral face, with the posterior interradius towards the observer. Cover-plates are preserved in all the rays, but are pressed into the grooves. × 2 diam.

Fig. 2. The adcentral region of the posterior interradius, showing the hydropore. × 10 diam.



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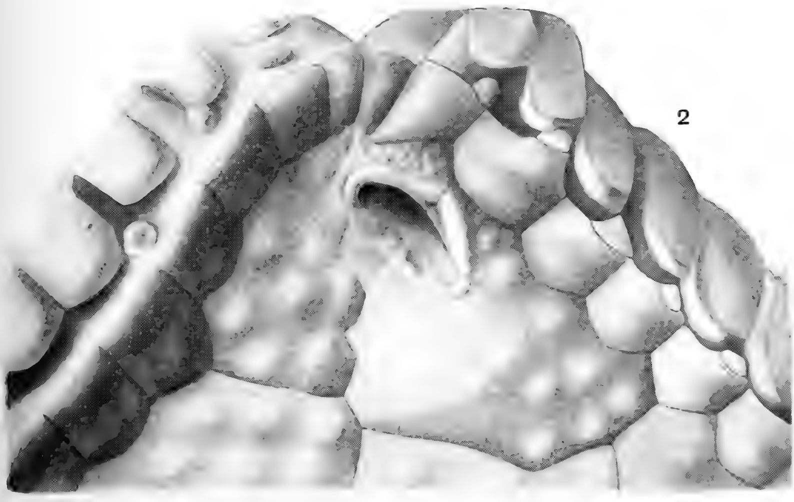

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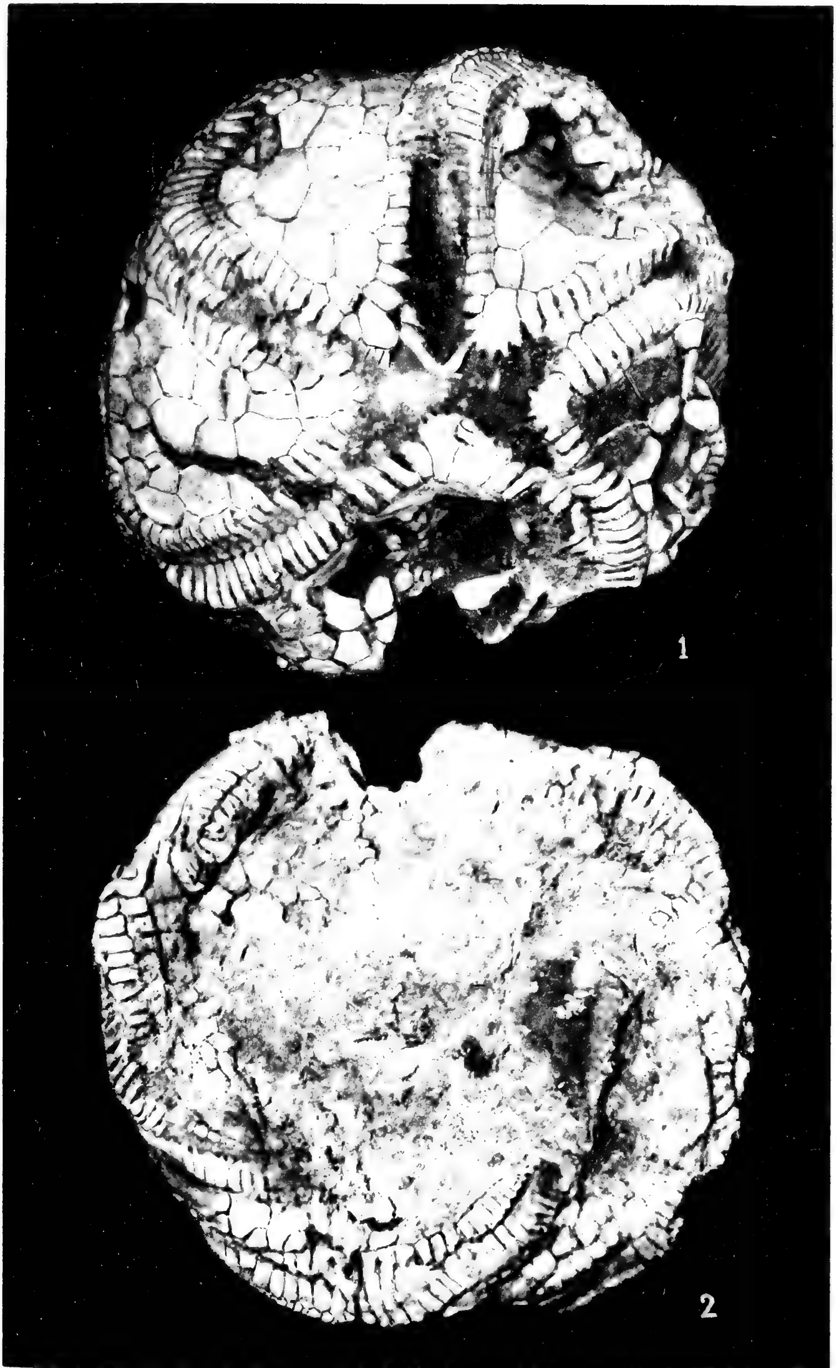
EDRIOASTER BIGSBYI.

Plate XII.

Edrioaster levis. Holotype (Brit. Mus., E 15900). × 2 diam. These photographs were taken under water, so as to bring up the sutures and the fragments of plates, which are seen with much difficulty in the dry state.

Fig. 1. Adoral face. The small periproctals are seen depressed in the posterior interradius, next the observer.

Fig. 2. Adapical face. This shows the peripheral course of the grooves. The frame and the plated integument within it cannot be distinguished.



Herring photo. London Stereoscopic Co.

EDRIOASTER LEVIS.

IV. The Edrioasters of the Trenton Limestone.

[Part II.]

[Geol. Mag., n.s., Dec. VI, Vol. I, pp. 162–171, Pls. XIII, XIV; April, 1914.]

THE Cover-plates of the radial grooves are preserved here and there in specimen A, notably over the oral centre (Pl. X, Figs. 1, 2, 5, 7, 8), but in B they are preserved over the whole of the grooves and the mouth, though pressed down on to the floor of the grooves and into the peristome (Pl. XI, Fig. 1). Cover-plates are also present in the British Museum specimens, and are almost complete in E 16054.

Each cover-plate corresponds in position with a floor-plate; so that, like the floor-plates, the cover-plates form a double series of alternating plates meeting in a zigzag median suture. The almost straight or slightly rounded outer margin of each cover-plate fits into a bevelled facet just within the rounded edge of the radial groove where the floor-plate begins its downward slope (Pl. X, Figs. 5, 7). This feature is well shown in specimen B, and there the floor-plate also shows, on each side of the facet, and distinct from the peripodium, a slight depression, possibly for the insertion of a muscle or ligament, or possibly for the reception of the accessory cover-plate shortly to be described.

From their facets the cover-plates stretch across the radial groove, either in a straight line (Pl. X, Fig. 5) or slightly arched upwards. Often, however, as in B, they have been pressed down into the groove, whether by contraction of tissues after death, or, as is more probable, by the pressure of the superincumbent rock.

The cover-plates abut closely, in tessellate fashion, when closed in the normal position over the radial groove. When pressed inwards, however, as in B, they have sometimes been made to imbricate with adoral overlap. This suggests a possibility of the converse action, namely, that in life they may have assumed a similar imbricate arrangement when they opened outwards, thus forming a slight gap between adjacent plates.

A gap may also have been produced by the opening of the accessory cover-plates. These are minute triangular plates frequently to be observed, one at the outer end of each suture between adjacent cover-plates, and therefore lying just over the pore (Pl. X, Fig. 8). Minute depressions in the floor-plates have already been mentioned as possibly the facets for their reception. These accessory plates are not always to be distinguished, but this may in some cases be due to the state of preservation, and the difficulty of detecting the sutures bounding such minute structures. When clearly seen, it is obvious that they were definite elements demanding explanation, and not caused by accidental cracks.

On the other hand, there is in E 16054 an occasional appearance of separate small plates along the median suture. In this case the appearance is probably due to fracture. The specimen has been

crushed, but the arched cover-plates, instead of being pushed into the groove, have resisted the pressure and given way at the summit of the arch.

Here we may turn to the differences presented by the subvective skeleton of *E. levis.* The floor-plates are not separated from the interradial plates by a continuous line of curved sutures, but join them by irregular angular sutures, varying in accordance with the outline of the plates against which they abut. And, just as they merge in this way into the interradials, so are they not distinguished from them by so sudden a rise above the general level as is the case in *E. bigsbyi.* Thus the rays of *E. levis* are less conspicuous, and, by reason of this as well as of their more regular curvature, have not that curious appearance of independent life.

The relations of the floor-plates to the cover-plates are also slightly different. A single cover-plate, instead of abutting on a single floor-plate, abuts as a rule on two. Consequently each floor-plate, instead of a single curved facet for its cover-plate (with a possible minute facet at each side thereof for an accessory plate), has one long curved facet for the cover-plate hinged to it, and a very short straight facet where the adjacent cover-plate plays against it. The longer curved facet, where distinctly observed, is on the distal side of the floor-plate. There are no accessory plates.

On the floor of the groove, the perradial zigzag channel is less marked, and the side-branches from it less pronounced. The surface of the plates between these branches is gently rounded, almost flat, and not ridged. The outer pore-depression and the inner, more adradial, depression are well marked, but not very distinct from one another. The specimens do not yield convincing evidence for or against the passage of pores to the interior.

The appearance of additional cover-plates along the median line is very strongly marked in certain regions of E 15900 (Text-fig. 2). These regions are just where the ray curves more sharply and passes along the periphery, and is therefore most subjected to both natural torsion of the cover-plates and post-mortem pressure. The former force seems to have induced an adcentral bending of the cover-plates as they approach the median line, and this is best seen towards the proximal end of the disturbed region (Fig. 2, II). Nearer the periphery the latter force has compressed the grooves so that the cover-plates have been raised, as in E 16054, and pushed together. Consequently their adcentrally directed ends have been broken across, and in some places seem to form a double row of small plates, alternating with each other and with the main cover-plates from which they are derived (distal end of Fig. 2, II). Occasionally each of these small plates is again divided by an apparent suture transverse to the median line of the groove, so that two small plates go to each main cover-plate (Fig. 2, III). The regularity of these appearances is diminished in proportion as the specimen is cleaned and carefully examined. None the less, the divisions between the plates look like true sutures, and they may represent a structure that arose naturally during life rather than the consequence of some accident or of post-mortem pressure.

Tegminals.—In both species, where the grooves meet at the peristome the cover-plates continue round them, and so form a roof over the actinal centre. No special plates are developed here, but all are serially homologous with the other cover-plates and have, in *E. bigsbyi*, the same accessory plates. There are, however, two differences: (1) in order to cover the space, these plates are rather larger and less regular in shape than normal cover-plates; (2) they appear suturally united to form a solid tegmen, and in consequence are rarely pressed into the mouth-cavity as in B, but are frequently preserved in place even when the other cover-plates have disappeared (Pl. X, Fig. 1).

The Peristome, which lies beneath this tegmen, consists of a roughly circular opening, surrounded by a frame. Owing to the persistence of the tegminal plates, the peristomial structures are rarely well shown, but it has proved possible to develop them on the right side of specimen A (Text-fig. 3). Here the floor-plates of one side of the right posterior ray curve round the right posterior interradius and meet those of the adjacent side of the right anterior

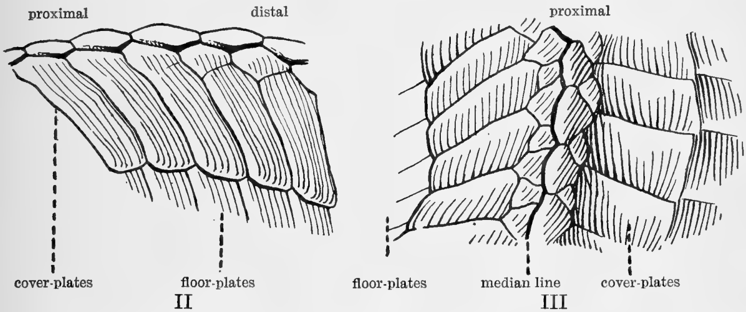


Fig. 2. Cover-plates of *Edrioaster levis*, from the adoral face near the periphery of the holotype. × 6 diam.

II. From the left anterior ray, showing the curvature of the admedian tract and its gradual change into a distinct plate.

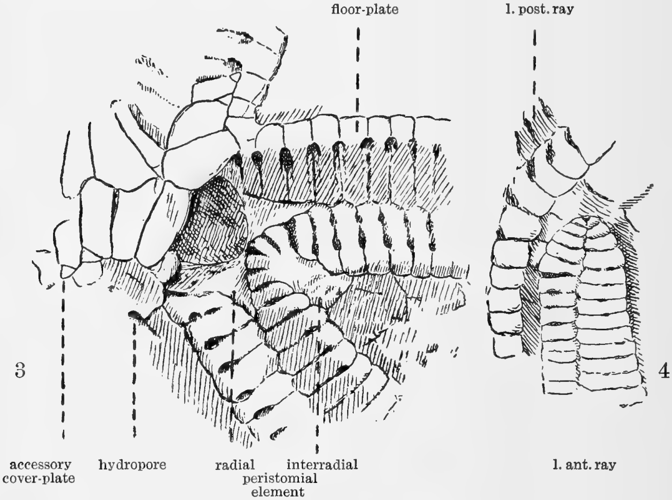
III. From the anterior ray, showing small plates similar to those in II, but with yet smaller plates between them.

ray, so that there is a fan-like arrangement of the pore-bearing sutures about the interradius. Four of these plates, two from each ray, appear to be fused at their marginal ends; and the solid plate thus formed stretches centrifugally along the interradius, serving as a fixed abutment for the adjoining floor-plates to the number of 2½ on each side. In other specimens five floor-plates may compose this interradial plate. Rarely, as in E 16172, there are two such compound plates formed in an interradius. These plates were noticed by E. Billings (1854, p. 273), who doubted whether their pores penetrated to the interior, but observed and figured a pore in the posterior angle as larger than the others.

As the floor-plates curve round to meet those of the next radius, they become separated from the corresponding floor-plates on the opposite side of their own radius. Between the two rows on the floor of the groove, there seems to be intercalated another skeletal

element, over which the groove itself passes centripetally down into the thecal cavity. As seen from above each of these radial flooring elements has a roughly triangular outline, and meets its fellows to left and right by its basal angles, thus forming a continuous ring round the central space. In 1854 (p. 271) E. Billings figured these plates as seen from the interior (fig. 11) and in section (fig. 12). He described them as triangular, and partly covered by the plates at the interradial angles, and as having "an elevated border on the side next the mouth, below, caused by the bending down of the plate."

To obtain a clearer idea of the relations of these apparent radial mouth-plates, I have removed the adapical structures and the matrix from the under side of rays III and IV in the peristomial region of E 16172. After three months of this labour it has been possible to produce Fig. 2 of Plate XIV, but the structures are still rather



Edrioaster bigsbyi. Specimen A.

Fig. 3. Portion of the peristomial region more developed by preparation than in Plate X, fig. 1. × 4 diam.

,, 4. The distal end of the left anterior ray, showing floor-plates only. × 4 diam.

difficult of interpretation. The peristome, as viewed from the inside of the test, is surrounded by a stout frame forming an elevated border. This border is flattened rather curiously, and is widest on the perradii, so that while its inner or adcentral margin is approximately circular, its outer or adperipheral margin approaches a pentagon with radial angles. The interradial tracts of this mouth-frame are, it is clear, composed of those floor-plates which, as already described, are fused to form the adoral or proximal interradial plates. The pores between these plates penetrate to the interior all the way round, though they decrease in size as they near the interradius. The radial tracts of the frame likewise seem to be composed of the floor-plates, which are here enlarged at their perradiad ends. There do not seem to be any

distinct interradial elements, but the appearance of such in external view, as described above, is almost certainly due to the overlapping of the perradiad ends of the proximal floor-plates. The difficulties of interpretation are due to the very close union of the plates to form a rigid mouth-frame, and to the cracks that develop during the process of preparation.

There appears to be in each ray some slight projection of the interporal region of a pair of floor-plates, each forming a process directed away from the perradius, and placed at the spring of the elevated border. These are not so regular that one can infer their normal and constant presence in every ray of all individuals, but they may well have some significance as processes for the attachment of muscles or other internal organs.

There are no traces of any other hard mouth-parts or of any skeletal connexion between the mouth-frame and the lobes of the adapical integument.

These peristomial structures are the stereom counterpart of the various channels and cavities observed in the internal cast of *Edrioaster buchianus*, and confirm the interpretation of those cavities offered in Study II, pp. 197, 198. Their relations to the soft parts will be discussed later.

The Interradial Areas are irregular in shape according to the varying curves of the radial grooves. In A, the posterior area, from the concavity of the left posterior ray to that of the right posterior, is 19·5 mm. across; but a part of this is occupied by the recurved end of the right posterior groove. Of the other areas, the widest is the left anterior, which measures 13 mm. at its widest part; and the narrowest is the right posterior, which measures about 7·5 mm. near the periphery (Pl. X, Fig. 1). In B the same general relations obtain (Pl. XI, Fig. 1). In E 15930 the chief difference seems to be that the left anterior area is relatively wider. In *E. levis*, on the other hand, the relations, owing to the solar curvature of all the rays, are quite different; thus, in E 15900 the measurements are: posterior, *circa* 24 mm.; left and right anterior, both 12 mm.; right posterior, *circa* 16 mm. (Plate XII).

The Interradial plates are irregular polygons, apparently with no definite arrangement. A single plate of moderate size abuts on the compound interradial element of the peristomial frame and is usually bordered by about four floor-plates on each side. This is followed by a number of plates different in each interradius. Thus in A the numbers are: l. post., 2; l. ant., 3; r. ant., 4 or 5?; r. post., 4. In B these plates almost agree in numbers and arrangement with those of A. In these two individuals the curvature of the rays is almost exactly the same, and there is also a remarkable general similarity in the number, shapes, and arrangement of the interradial plates. This similarity may imply either that the plates are heritable morphological elements, or that similar mechanical causes acting upon an indifferent plate-forming tissue have produced a similar breaking-up of the stereom. That the latter is the true interpretation seems to be proved by the other specimens, for in them the same plates cannot be identified.

The interradial plates are stout, those not far from the periphery in E 15930 having a thickness of 1 mm. and over. They are tessellate, with vertical sutures, but, as already described, dipping with oblique sutures under the radial floor-plates. There are no pores through or between the plates. The surface in well-preserved tracts is coarsely pustulate (Pl. XI, Fig. 1). The pustules are distinct, and spring from an irregularly reticular surface. E 16054, being a small and presumably a young individual, shows the pustules rather faintly and of smaller size than in the other specimens; a large proximal plate in the left anterior interradius has the pustules distributed about 9 to 1·5 sq. mm. In E 15930, an individual of more than twice the diameter, the pustules on a similarly placed plate run about 9 to 3 sq. mm.

These pustules are not due to the breaking up of growth-lines by radial stresses, but they may very well have been tubercles bearing minute spines. Such spines, being very loosely attached, would readily fall off after death, and would in any case escape observation owing to their minute size. I have searched for them in the very small amount of available material, but in vain, unless a tiny rod (·8 mm. × ·25 mm.) in the left anterior interradius of E 15930 may possibly be one.

The specimens of *E. levis* differ in having no distinguishable pustules, a feature to which my attention was first directed by Mr. Walter Billings. The exposed surface of these two specimens has been somewhat worn (one had apparently been trodden on), and this has exaggerated the smoothness. When other parts were freed from their protecting matrix they presented a surface that might be described as slightly vermiculate, or perhaps more accurately as 'scrobiculate'.

The Anus is well shown in specimen A (Pl. X, Fig. 1). It lies between the distal end of the right posterior groove and the bend in the left posterior groove, and is surrounded by a number of small plates, which must have lent greater flexibility to the test in this region. Twelve of these plates meet round the actual opening, from which the sutures between them radiate (Pl. X, Fig. 9). They are not of equal length or width, and meet the smaller surrounding plates quite irregularly. There is no imbrication. The area covered by small plates rises up in a slight dome above the general level of the interradius, but at its summit is again pushed in just round the anal opening, possibly in consequence of post-mortem contraction. The anal dome is not sharply defined on its right side, but seems continuous with a general swelling of the thecal surface in that direction. The rectum may have lain under here, and this, if so, would indicate that the gut had a dextral coil. The similar appearances in *E. buchianus* have received a similar interpretation from Professor Jaekel and myself (cf. Study II, p. 199).

In specimen B (Pl. XI, Fig. 1) the periproctal plates are disturbed, but the dome is discernible, as also the swelling on its right. In the two specimens of *E. levis* the periproctals are numerous and small, but do not appear to be elongate to any considerable extent.

The Hydropore, or at least the thecal opening which I thus identify,

lies at the adoral end of the posterior interradius, close to the margin of the right posterior groove. It is clearly seen in specimen A (Pl. X, Figs. 1 & 7) and B (Pl. XI, Figs. 1 & 2), and indeed can always be recognized whenever that portion of the test is plainly exposed. Its normal appearance is that of a small, slightly curved slit, approximately parallel to the right posterior ray. Its length is 1·1 mm. in A, 1·5 mm. in B. It widens slightly towards its adoral end, deepening at the same time, and becoming darkened with matrix, an appearance that indicates an oblique passage of the canal through the test. Specimen B shows the margin of the slit raised in a rounded rim, well defined at the adoral end and along the right side, but broken up into lobes on the other side. The slit is contained in two plates, and crosses the suture between them at right angles. The actual canal is only in the adoral of these two plates, and it may be that this plate is homologous with the interradial elements formed by the fusion of the peristomial floor-plates; but all the plates in this region are so closely united that the sutures are hard to trace. The tract of the adoral plate between the rim of the hydropore and the rounded margin of the peristomial floor-plates bears, in specimen B, about fifteen minute, closely-set pustules. Spinelets, if attached to these, would have provided a filter for the inflowing water.

Specimen E 15930 seems to show a slight branching of the slit, such as occurs during ontogeny in the very earliest stages of the folding that forms the madreporite of a recent Echinoid or Asteroid. Such branching increases the ciliated area by which the water-current is driven. The hydropore was not mentioned by E. Billings at any time, but his restored figure (1854, Fig. 10) shows that he observed something in the region where we now know it to occur.

The Under or Adapical face has been exposed by patient preparation in specimen A (Pl. X, Fig. 3), but is better shown in specimen C (Plate XIII). It is bounded by the distal halves of the four sinistrally curved radial grooves, which, as seen from below, of course appear dextral or solar. Their ends are quite definite, as described above (Text-fig. 4); when Plate X was drawn, some twelve years ago, they were still obscured by matrix, which has since been removed. The concave space included by these may, as in *E. buchianus*, be divided into three regions: the Peripheral Area, the Frame, and the Central Area.

The Peripheral Area is formed by a ring of plates serially homologous with the interradials of the upper face, and, in specimen A, connected with them by a single row of small plates passing between the rays. These peripheral plates of the under face are a little smaller than the majority of the interradials, and form, in specimens A and C, a single row, occasionally doubled, bordering the rays. In E 16173 (*E. levis*) these plates are relatively smaller than in A and C, and occupy a relatively wider belt, so that on both counts they are more numerous; they differ further in being more distinctly of two sizes, namely, larger plates with smaller ones surrounding or intercalated between them.

The Frame is a ring of larger and thicker plates (see the section, Pl. X, Fig. 9), the number of which appears to have been twelve in C,

and probably the same number, not more, in A. In *E. buchianus* eleven such plates were counted, but the general shape and arrangement are the same in the two species. The inner margin of each frame-plate in *E. bigsbyi* is straight or concave, not convex as in *E. buchianus.* I have not observed on them any sign of tubercles or pustules, such as appear to have existed in *E. buchianus.*

The Central Area, in all specimens where any portion of it can be seen, is darker in colour and irregularly wrinkled (Pl. X, Fig. 11). It was doubtless covered by a flexible integument, filled with minute plates, which it has been possible to observe, though not clearly to photograph, in some tracts of specimen C (Plate XIII) and in E 16172 and E 15930. This scaly skin was attached to the frame-plates, and may as a rule have spread over them to some extent, especially at the sutures between them. The minute plates were tangentially elongate, and when closely pressed together, as in the folds, tend to project and to imbricate.

The adapical face of E 15930 (Pl. XIV, Fig. 1) differs from that of all other specimens observed in the apparent absence of a frame: the plated integument seems to stretch right up to the peripherals. In the region that should be occupied by the frame there are, however, appearances as though the integument had been thrown into raised circular or crescentic folds, each bounding a strongly pustulate floor. It may be that this floor is formed by the fusion of small plates, or that it indicates a frame-plate underlying the plated integument.

In cleaning away the matrix, it was peculiarly interesting to discover in these species the lobed central evagination, which I first made known in *E. buchianus.* Its pentagonal shape is not so obvious here. In A it is roughly triangular, with a short base in the left anterior interradius, and two long sides directed to a distinctly folded apex in the right posterior radius. One of these sides may be regarded as containing the lobes of the right anterior and right posterior interradii, and the other those of the posterior and left posterior interradii. In C (Plate XIII) the irregular lobate edge of the posterior half of this evagination is clearly seen, and we are perhaps justified in distinguishing the lobes of the three posterior interradii.

Prolonged preparation and repeated examination of the area surrounded by the lobes in A, C, and E 16172, have convinced me that there was no central opening of a permanent nature, such as E. Billings mentioned as apparently present (1854, p. 272). Neither is there evidence for pores of any kind in any part of the adapical face. It is perhaps hardly necessary to add that there is no sign of any stem or root, unless the central lobed region be regarded as in some sense the homologue of a stem.

Discussion of the physiological and morphological meaning of the structures herein described is reserved until, in a forthcoming Study, the structure of *Steganoblastus* shall have been redescribed. At this point, however, the distinctive features of the genus *Edrioaster* and of its four known species may be resumed in the following diagnoses.

Family EDRIOASTERIDÆ.

Edrioasteroidea with a theca composed of separate and relatively thin plates, and apparently without permanent attachment; with a subvective skeleton partly visible in apical aspect, and composed of floor-plates and movable cover-plates, having pores between the floor-plates; interradials of oral face continuous with those of apical face; central area of apical face covered with more flexible integument, bearing smaller plates; a hydropore (probably always) pierces an adoral interradial of the posterior interradius.

The genera are *Edrioaster* E. Billings, 1858; *Aesiocystis* Miller and Gurley, 1894; *Dinocystis* Bather, 1898; *Lebetodiscus* Bather, 1908.

Aesiocystis comprises a single species, *A. priscus*, based on four imperfect specimens from the Trenton Group of Mercer Co., Ky. (Bull. Illinois State Mus. Nat. Hist., No. 5, p. 13, pl. ii). The genus was placed by its authors in the family Hemicystidæ, but their description and figures show that it was almost certainly an Edrioasterid; indeed, my chief doubt is whether the species was not actually an *Edrioaster*.

Edrioaster.

An Edrioasterid with pores of subvective groove within the tract protected by cover-plates; with interradials all tessellate and separated from the central apical region by a frame of stouter plates; on the apical face the peripheral plates are variable in size but not minute, the central plates are minute and tend to imbricate.

Edrioaster bigsbyi E. Billings.

An *Edrioaster* with height of theca about one-third of diameter, periphery roughly circular; with rays clearly raised above general surface, and floor-plates clearly demarcated from interradials; rays I, II, III, IV have a contrasolar curve, ray V a solar curve, ray IV bends upwards within r. ant. interradius; interradials of oral face bear coarse, sparse pustules.

This is the genotype.

Edrioaster buchianus E. Forbes sp.

An *Edrioaster* with height of theca one-half the diameter or more, periphery sub-pentagonal with convex interradii; with rays apparently not raised above general surface, but with floor-plates clearly demarcated from interradials; rays all have a solar curve; interradials slightly pustulate?

Edrioaster saratogensis Ruedemann.

An *Edrioaster* with depressed theca (height probably about one-fourth diameter), periphery sub-circular to sub-pentagonal with convex interradii; with rays clearly raised above general surface, and floor-plates not regularly demarcated from interradials; rays all have a solar curve; interradials relatively few, and all, as well as cover-plates, densely and finely granulose.

This diagnosis is based partly on the description and figures of Dr. Ruedemann (1912, Bull. N.Y. State Mus., No. 162, p. 86, pl. iii), partly on squeezes which he was so kind as to send me. Dr. Ruedemann, apparently being acquainted with none of my previously published

work on *Edrioaster*, naturally found difficulty in describing his imperfectly preserved specimens. The subvective skeleton has the normal *Edrioaster* structure, and the so-called 'subambulacral plates' marked '*a*' in pl. iii, fig. 4, are incorrectly drawn. The absence of evidence for a contrasolar ray has already been alluded to (p. 122). The 'triangular oral plates' are presumably the interradial elements of the mouth-frame. The cover-plates slope from their outer margins towards the oral pole; those pushed into the groove tend to imbricate adorally.

The original specimens came from sandstone in the Snake Hill shales of Saratoga Co., N.Y. These beds are supposed to lie just above the Basal Trenton, and below the *Prasopora* zone. The species is therefore the oldest of the four here discussed.

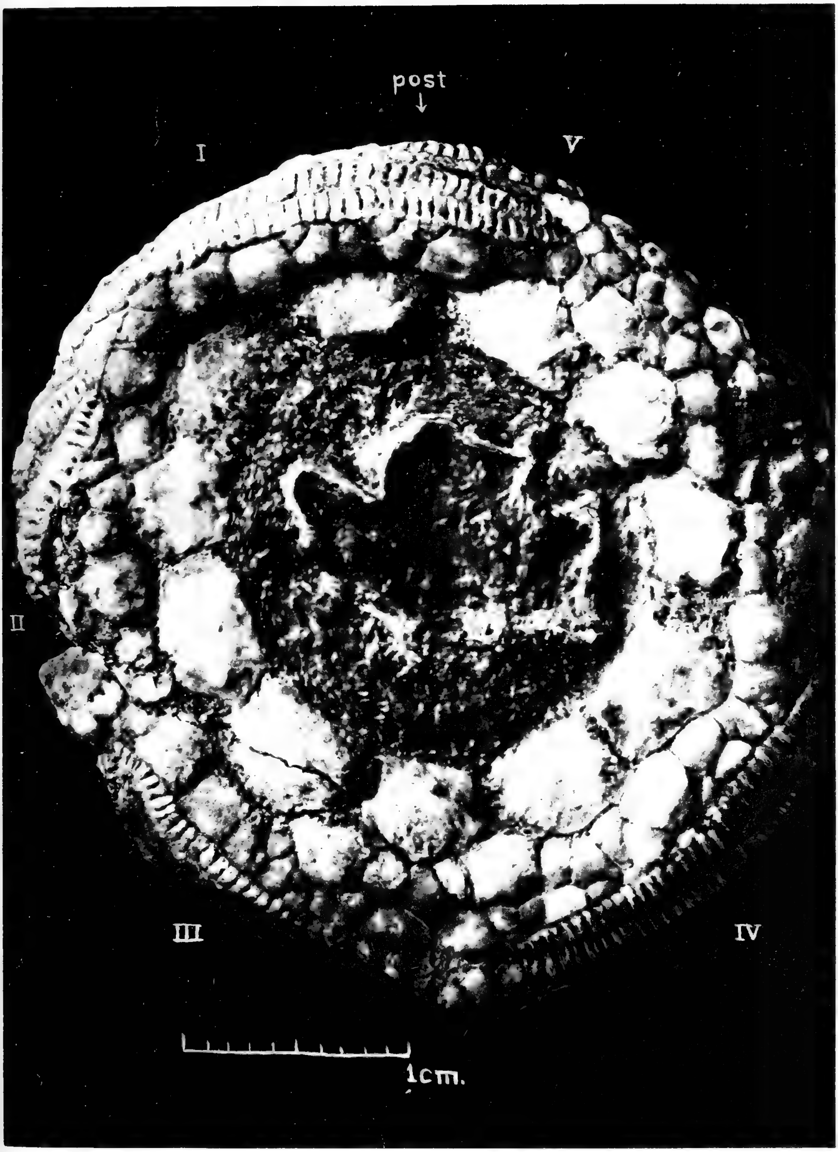
Edrioaster levis n.sp.

An *Edrioaster* with height of theca about one-third of diameter, periphery roughly circular; with rays scarcely raised above general surface, and floor-plates not clearly demarcated from interradials; rays all have a solar curve; interradials faintly scrobiculate, not pustulate.

Holotype, Brit. Mus. E 15900.

Plate XIII.

Edrioaster bigsbyi. The adapical face of specimen C, of the Canadian Geological Survey, showing the peripheral portions of rays I–V, the eleven large frame-plates, and the lobed evagination of the central integument, the small plates of which are not clearly seen. × 3 diam.



Herring photo. London Stereoscopic Co.

Edrioaster bigsbyi.

Plate XIV.

Edrioaster bigsbyi.

Fig. 1. The adapical face of E 15930, with same orientation as Plate XIII. The minute plates of the central integument are well shown. In the place of the frame are the circular elevations of this integument described on p. 169. Photographed by Mr. H. G. Herring. × 3 diam.

Fig. 2. Part of the circumoral region of the test of E 16172, seen from the interior, as described on p. 165. Drawn by Mr. W. G. Browning. × 3 diam.

Fig. 3. Some floor-plates of E 16172, showing the ridges that lead from the peripodia to the perradial channel. Drawn by Mr. G. C. Chubb. × 10 diam.

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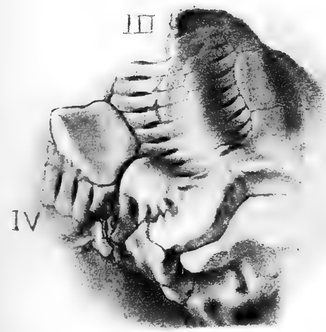

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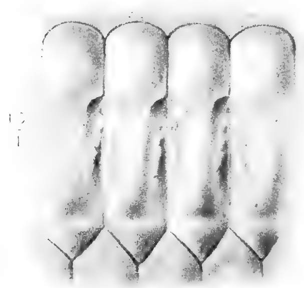

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EDRIOASTER BIGSBYI.

V. *Steganoblastus.*

[Geol. Mag., n.s., Dec. VI, Vol. I, pp. 193–203, Pl. XV; May, 1914.]

Previous History.

This form was first made known in 1897, by the late J. F. Whiteaves, in a paper entitled "Description of a new genus and species of Cystideans from the Trenton Limestone at Ottawa" (Canad. Rec. Sci., vol. vii, No. 5, pp. 287–92). This part bears on the wrapper the date "January, 1897", which is obviously erroneous, since the author dated his own contribution "April 28th, 1897", and copies of it were first received in London on July 31 of that year.

In that paper the species received the name *Astrocystites ottawaensis*, and was regarded as "most nearly related to *Asteroblastus*, Eichwald, and . . . probably referable to the same family". In a letter sent to Dr. Whiteaves by the next mail, I pointed out difficulties in this interpretation of the structure, as well as difficulties in the name *Astrocystites*. "You can," I wrote, "hardly have been aware that Haeckel, in 1896, separated *Asteroblastus tuberculatus* of Schmidt from *A. stellatus* under the new generic name of *Asterocystis*." I further pointed out that the termination *-ites* was frequently dropped, and was no real distinction; also that ἀστήρ and not ἄστρον was the correct word to use in composition for the sense intended by Dr. Whiteaves. A change of name therefore not only would avoid confusion but seemed to me justified. Dr. Whiteaves accepted my view, and in a "Postscript" (tom. cit., p. 395, January 7, 1898) published the name which I suggested to him—"*Steganoblastus*, from στεγανός, closely covered, with reference to the large covering plates and covered mouth." In this Postscript he inadvertently alluded to the species as *Steganoblastus canadensis* instead of *S. ottawaensis*.

In consequence of my remarks on the structure, Dr. Whiteaves kindly lent me the two specimens belonging to the Geological Survey of Canada, which, with an imperfect specimen lent me by Mr. Walter R. Billings, made up all the known material. The first results of my examination were summarized in Lankester's *Treatise on Zoology*, vol. iii, pp. 209–10, text-fig. vii (1900), where I founded for the reception of this genus the Family Steganoblastidæ of the Class Edrioasteroidea.

In September, 1906, Dr. Whiteaves reprinted his original description, followed by a complete extract from the *Treatise*, in *Palæozoic Fossils*, vol. iii (pp. 316–21), published by the Geological Survey of Canada. My drawings of *Steganoblastus* were also among the very large number of text-figures which Messrs. Delage and Hérouard paid me the great compliment of reproducing in reduced facsimile in their *Traité de Zoologie concrète*, tome iii, "Les Echinodermes" (pp. 415, 416, Paris, March 30, 1904). The Family Steganoblastidæ is accepted by Dr. F. Springer in the second edition of Eastman's *Zittel* (1913).

The present paper gives the evidence on which my textbook account was based.

Material.

The specimens are the three syntypes of Whiteaves, and may be distinguished as A, B, and C. All were obtained from the Trenton Limestone at Division Street, Ottawa. The precise horizon has nowhere been stated.

Specimens A and B were collected by Mr. John Stewart in 1886, and are in the Victoria Memorial Museum, Ottawa. Specimen C was collected by Mr. Walter R. Billings, in whose possession it remains.

A is an almost perfect theca with two columnals. It is the original of Whiteaves' figs. 1 and 2, and of Pl. XV, Figs. 1, 3, 4, 6, 7, in the present paper. It is hereby selected as the holotype.

B is a theca crushed in the left anterior interradius and adjoining radii, with portions of three columnals. It is the original of Whiteaves' fig. 3, and of our Pl. XV, Figs. 2, 5.

C is a much broken and crushed theca with no columnals.

"All three of these specimens, when found, were," says Whiteaves, "almost completely covered with a very tenacious shaly limestone." This had been for the most part skilfully removed before the specimens were sent to me, but the pores and the outlines of the plates were still obscured.

General Description.

The chief features can readily be gathered from the slightly restored figures 1 and 2, here reprinted, with slight modification, from the *Treatise* (1900).

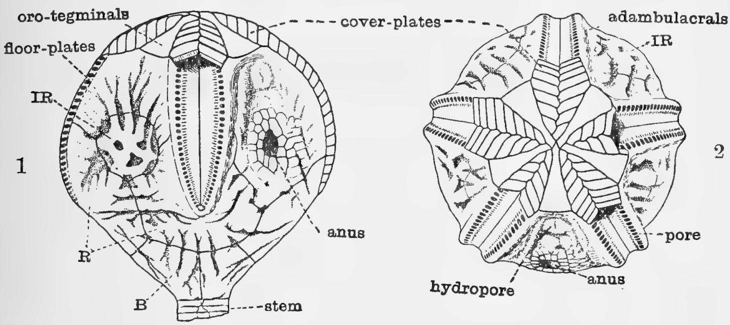
The most obvious difference from Edrioasteroidea belonging to the Family Edrioasteridæ lies in the Stem of normal pelmatozoan character. This supports a Theca of regular pear shape.

The Theca consists, as in other Edrioasteroidea, of two systems of plates: (1) an adoral system, (2) an adapical system. From the tegminal region above the peristome, the Adoral System radiates in the form of five subvective grooves, passing straight along the perradial meridians, to a level almost exactly two-thirds of the way down the long axis of the theca. From the stem, at the opposite pole, the Adapical System spreads upwards, supporting and passing in between the five grooves, to abut finally on the interradial elements of the tegmen. In one of the interambulacral areas of this system, lies the anus, marking the posterior interradius

Description of the Specimens.

The measurements of the piriform theca in specimen A are approximately: height, 19·5 mm.; greatest diameter, 18 mm., this being at 8·5 mm. from the summit.

Except for the tegminals and cover-plates, all the thecal elements are closely united, so that it is difficult to distinguish the sutures. This difficulty is enhanced by the pitted ornament of the surface, and by the very deep folding of the plates which form the adapical system. On the other hand, as one removes the tenacious black matrix from the depths of the folds, one realizes that they represent a system of rhomb-ridges and axial folds on the plan so common in Pelmatozoa; and, remembering that in such cases the folds are at right angles to the sutures, one is able with somewhat greater confidence to trace the limits of the plates. In some cases it may be that the arrangement of the folds indicates rather the original constitution of the young individual (or of its ancestor) than any actual



Steganoblastus ottawaensis.

Fig. 1. Restored view of theca from left posterior interradius.

Fig. 2. Restored view of oral surface.

Both drawings are based mainly on specimen A. × 2 diam.

separation of plates in the adult. It seems plain that the tendency of the species is to fuse the originally indefinite smaller plates into a few larger plates of definite arrangement (cf. Text-fig. 3).

The plates distinguishable in the adapical system (Text-fig. 1) are five basals, five radials, and in each interradius a varying number of interambulacrals. From a strictly morphological standpoint, one should perhaps also include in this system the floor-plates of the subvective grooves.

The Basals are of the pentagonal shape usual in normal crinoids. As the following measurements from specimen A show, they are a little lower on the posterior side of the theca, owing to the space required by the anal plates. The measurements are in millimetres and are taken along the surface of the theca.

	l. ant.	l. post.	post.	r. post.	r. ant.	ant.
Height of basal	5·6	5·5	5·1	5·2	5 7	
Height of interbasal suture	4·6	4·0		3·5	4·2	4·25

The Radials are of the roughly pentagonal shield-shape usual in normal crinoids and in blastoids. Since they have no brachial facet, but are notched for the excavation of the subvective grooves, they more closely resemble the radials of blastoids. The basi-radial and interradial sutures can be traced without excessive difficulty; the lengths of the latter, in the case of the anterior radial of specimen A, are left anterior 3·5 mm., right anterior 4 mm.

From the top of the interradial sutures, the shoulders of the radial slope upwards towards the subvective groove, and the sutures bounding them can be traced for some distance. The point at which they meet the flooring-plates of the groove cannot, however, be distinguished, owing to the close union of the various plates in the neighbourhood of the groove. Estimated roughly, for the anterior radial as before, the level of the top of the radial would be about 5 mm. from the lip, or distal end, of the groove; and the distance of the lip from the lower apex of the radial is about 4·1 mm.

The rhomboidal area above the shoulders of the radials and between the grooves is filled with Interambulacral plates. The precise number and arrangement of these varies in the different areas, and in all except the posterior area their outlines are hard to see (Text-fig. 3). To judge from the folds, three or four small plates have joined in the centre of each area, except the posterior, to form a relatively large plate of somewhat swollen appearance (IR). This plate rests on the radials, and other smaller plates lie between it and the grooves.

The posterior area, which is more swollen and a trifle wider than the others, measuring almost exactly 10 mm. from lip to lip of the bounding grooves, is filled with a larger number of plates. Except near the boundaries of the area, these are more loosely united, so that the sutures are readily seen. About the centre of this area in specimen A the plates are rather sharply depressed; but in B the corresponding depression is very slight, so that it has here proved easier to remove the matrix, and thus to disclose seven plates converging to a point, where doubtless was the vent. These seven Circumanal plates are surrounded by about fifteen other Periproctal plates, equally well defined, very diverse in shape but never long and tapering. Outside these again come plates less well defined and therefore less easily counted, but in total number about nine, one being interradial and resting on the radials, and four bounding the sides of the periproctal area and meeting above it in an interradial suture. The twenty-two periproctal plates are but faintly pitted, and each has an equably swollen surface. The nine bounding interambulacrals, however, are coarsely folded on their abanal margins, and the folds meet similar folds from the radials and from the adambulacral plates.

By Adambulacral plates I mean those which lie between the last set of plates and the grooves; but whether they are really distinct from the floor-plates of the grooves is uncertain. To this point we shall recur.

At the adoral end of the interambulacral area there lies in the posterior interradius, and apparently in the other interradii, a single

plate, continuous with the adambulacral series, and abutting above on the corresponding oro-tegminal. In the posterior interradius this plate occupies a larger area than in the others, and is much more swollen. Close examination under suitable illumination detects in this plate, in all three specimens, a meridional dark line. This is not a suture, for it is waved and does not reach the edges of the plate. It may represent the Hydropore.

The Ornament of the adapical system consists of the axial folds already mentioned, and of a number of pits.

The Axial Folds in the lower, proximal or adcolumnal region of the theca are fairly regular. From the lip of each radial there run four main ridges, one pair horizontally to the lips of the adjacent radials, one pair downwards to the middle of the base of the adjacent basals. These main ridges thus enclose triangular spaces, namely an almost equilateral triangle bounded above by the horizontal ridges, and interradial in position; an acute-angled triangle with its base on the columnar suture, and radial in position. The interradial triangle encloses a smaller, less regular triangle of ridges. The radial triangle encloses two shorter ridges also springing from the base and meeting at a wider angle (*circa* 90°) at about one-third the height of the radial triangle itself. The triangular interambulacral area, above the main horizontal ridge, contains ridges crossing the sutures of the various plates already described as interambulacrals and adambulacrals.

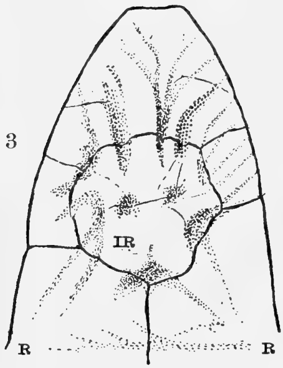
The folds between the ridges are very deep, especially in the interambulacral area, notably a fold just below the adoral interambulacral (Text-fig. 3). The removal of the matrix from these is extraordinarily difficult, and has therefore only been accomplished in one or two places. The operation led to no discovery of pores or any system of respiratory folds, and it may be inferred that the sole effect of the folding is to endue the theca with a quite exceptional rigidity.

The Pits cover the whole outer surface of the theca, including all the elements of the adoral system (Pl. XV, Figs. 2, 3). They have in many cases been worn away from the more prominent parts, either in the process of cleaning or, as there is some evidence to show, before the fossil was embedded in the matrix. They seem to lie even in the depressions of the folds, although not quite so well marked there. The pits seem to have been set most closely on the cover-plates and tegmen, and in consequence may there assume a more hexagonal outline. Elsewhere they are more circular. They vary in size, but have as a rule a diameter of about ·2 mm. Though they have no definite arrangement, they tend to lie along the edges of the cover-plates and along the sides of the larger folds. Occasionally there is a tendency to similar seriation at a definite angle to the sides of the grooves, as though marking the original adambulacral plates. These structures are pits, not pores, for one cannot imagine pores on cover-plates, and in any case they disappear entirely when worn down. No definite structure can be distinguished in them, but their complete resemblance to the spine-pits of Asteroidea and the lack of any other explanation render it highly probable that they lodged spines.

The Subvective System consists of five broad radial grooves leading to a subtegminal mouth. The grooves are bounded by Floor-plates,

one series down each side of a groove. The two series meet along the perradius in a distinct straight suture. In each series the floor-plates are united by a very close suture, or are even fused. The sutures can most readily be detected at the distal end of the groove, near the lip (Pl. XV, Fig. 3); but their former presence is clearly marked all the way up by a series of pores, similar to the pores between the floor-plates (so-called ambulacrals) of ordinary Asteroidea, and markedly resembling those in *Edrioaster*. That these structures are pores is proved, not merely by this external resemblance, but by distinct signs of their passage through the test wherever that is broken or ground away. The pores have an elongate-ovate outline on the surface, the broader end lying just below the edge of the groove, in other words just below the attachment of the cover-plates. The narrower end points towards the perradius, and merges into the suture between the floor-plates, which in its turn dies away before joining the perradial suture.

3



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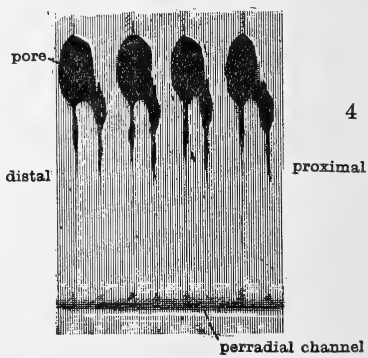


Steganoblastus ottawaensis.

FIG. 3. An interradial area of specimen A, to show the direction of the folds, and the occasional traces of sutures at right angles thereto. × 4 diam.

FIG. 4. Portion of the side of a subvective groove, to show the pores between the floor-plates, and the depressions on the floor-plates. × 16 diam.

In tracts that have not been so well cleaned from matrix as others there occasionally appears to be another series of smaller piriform pores, between the others, and nearer the perradius (Text-fig. 4). Further cleaning, however, shows that these are not pores but depressions. Each such depression is moreover connected with the pore on its distal side by a faint groove sloping downwards from the main pore to the piriform depression.

Below the pores and the piriform depressions, that is to say nearer the perradius, is a slight swelling of the groove-floor, so that a faint rounded ridge separates the poriferous tract from the smooth floor of the groove. In other words, there is a perradial channel. The sutures continuing the pores, and the channels continuing the piriform

depressions, cross this ridge at right angles, and so break it up into a row of rounded eminences, producing a toothed appearance.

At the distal end of the groove the floor-plates rapidly decrease in size, and this series is rounded off before the actual lip of the groove is reached. The distance between the end of the floor-plates and the lip seems to vary in the different radii. That in which best results have been obtained by preparation is the anterior groove of specimen A (Pl. XV, Fig. 3), but this is confirmed by other grooves so far as it has been possible to clean them. That the distal end of the groove was quite free of floor-plates is proved by the continuation of a double row of pits over the lip and along the middle of the groove, up to the end of the floor-plates. The sutures bounding these terminal floor-plates are distinct all round, and the floor-plates are seen resting on the grooved surface of the radial. Apparently, however, the radial does not actually pass right under the floor-plates, but is cut away beneath their adradial region, so that the pores between the floor-plates pass through into the thecal cavity.

The floor-plates in this part of the groove at any rate appear to have their outer boundary at the level of the pores. Owing to the close union of the floor-plates, not only *inter se*, but also with the radials and adambulacrals, it is impossible to trace any bounding suture along the edges of the groove. It seems, however, a legitimate inference that a generally similar relation of the floor-plates to the adjacent thecal elements prevails, or did in earlier stages prevail, all the way up the groove; at all events, it is clear that the floor-plates and adambulacrals are independent morphological elements, and this is a point of much theoretical importance.

At the distal end of the groove it is plain that the floor-plates of one side alternate with those of the other side.

The Cover-plates are best preserved in specimen B (Pl. XV, Figs. 2, 5; Text-fig. 5). In no case are they retained as far as the distal end of the groove, but there is no reason to doubt that they were continuous from the tegmen to the extreme end of the floor-plates. In the upper half of the right anterior groove, starting about one plate below the distal end of the oro-tegminal, there are nine cover-plates in a length of 5 mm. The proximal of these plates has a length of 2·5 mm.; the distal one a length of 1·8 mm. Nearer the oral pole the cover-plates are more irregular in shape and size, especially in this r. ant. radius of this individual. Over the greater part of the groove the cover-plates alternate regularly and meet in a zigzag suture; but at the proximal end smaller plates may be intercalated along the middle line. In specimen A there are no such intercalated plates, but the median suture in the proximal region becomes curved and interlocking (Text-fig. 6).

The relation of the cover-plates to the floor-plates appears to be quite regular. There is a cover-plate to each floor-plate, and, so far as can be ascertained after prolonged preparation and study, the sutures between the cover-plates coincide with those between the floor-plates. Thus the pores, which, as already stated, lie just below the attachment of the cover-plates, open under the sutures as in *Edrioaster*.

The thickness of the cover-plates about half-way down the r. ant. radius of specimen B is not more than ·35 mm. In many cases the cover-plates have been pulled or pressed down into the groove, but when preserved in what would seem to be their normal position they form a prominent rounded arch over the groove. The sutures between adjacent cover-plates, as well as the median suture, are slightly depressed and bordered by spine-pits. The suture between the cover-plates and the adambulacrals is flush, and the curve of the cover-plates passes over, though with a distinct bend, into that of the adambulacrals. The suture is not a straight line, but a series of curves, the convex outer edges of the cover-plates fitting into slight concavities in the adambulacral margin. The position and number of the axial ridges on this margin indicate that the original adambulacral elements coincided in number but alternated in position with the cover-plates, and therefore also with the floor-plates. This suture, then, is essentially a zigzag suture between two sets of alternating

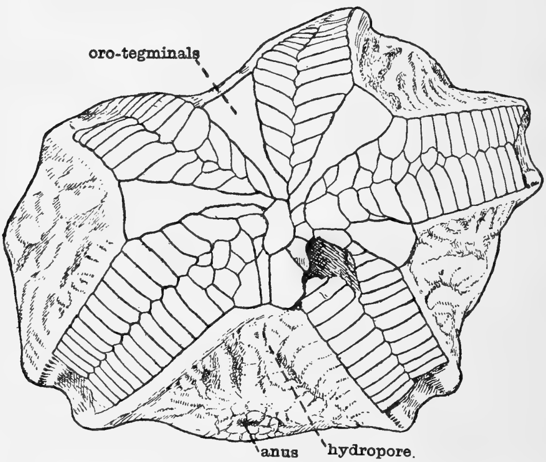


FIG. 5. *Steganoblastus ottawaensis.* Specimen B viewed from above, for comparison with Pl. XV, Fig. 5. × 4 diam.

plates. In consequence of this arrangement, one would expect to see along the edges of the groove, when the cover-plates are removed, a series of depressions or facets for the reception of the cover-plates. Unfortunately the edges have in nearly every case been worn enough to remove all trace of these very faint depressions, and it has only been by dissecting away some cover-plates at the end of the r. ant. ray in specimen B that I have been able to distinguish anything of the kind.

The Tegmen is best studied in specimen A (Pl. XV, Fig. 7; Text-fig. 6). Here the cover-plates are more regular than in B, and the arrangement of the whole follows an obvious symmetry, which, from its resemblance to that in other Pelmatozoa, must be regarded as the normal. In addition to the cover-plates, the tegmen contains

only five plates, which have already been alluded to as the oro-tegminals. These abut by their distal broader ends on the inter-ambulacrals, and gradually narrow as they pass, between the converging and narrowing series of cover-plates, towards the oral pole. As is usual in Pelmatozoa, only three of them meet there: the posterior and the right and left anterior. There is, however, a difference from the usual plan in that these three can scarcely be said to meet in a triradiate suture; but the posterior plate passes between the other two and with its pointed apex actually touches the proximal cover-plate of the anterior radius, so that in this individual the two anterior oro-tegminals do not touch one another as is customary and as they do in specimen B.

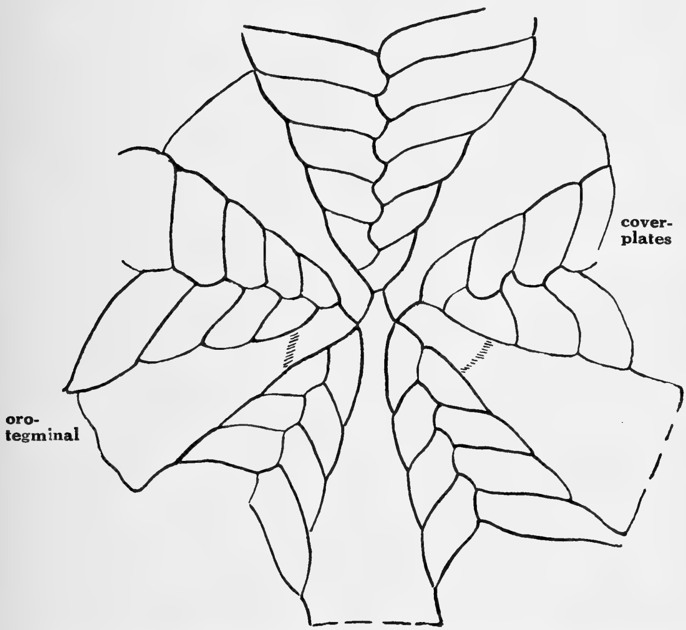


FIG. 6. *Steganoblastus ottawaensis.* Exact drawing of the sutures in the tegmen of specimen A. × 8 diam.

These three oro-tegminals have the same general shape. Each tapers gradually as the subvective grooves bounding it converge, then, as the grooves are rounded off, it expands, and again tapers rapidly to a sharp point, thus resembling a spear-head. Each of these three plates appears to be one continuous element, from the pointed apex to the broad straight base.

The two other oro-tegminals, the r. and l. post., are of the same general shape, except that they do not end in a spear-head, but in an oblique suture, abutting on the adjacent side of the spear-head of the r. and l. ant. oro-tegminal respectively. At the extreme end of this

suture they may just touch the post. oro-tegminal. It is not so certain that these two plates are continuous elements. They seem to be crossed by an obscure oblique suture at the level of the second cover-plate of the adjoining grooves. It is not impossible that the proximal portion of each of these plates may represent the proximal cover-plate of the l. ant. and r. post. grooves respectively. Those are the grooves to which the supposed cover-plates would naturally belong, in spite of the asymmetry involved.

The tegmen of specimen B is so much more irregular and asymmetrical that it cannot be described in detail. The r. and l. ant. oro-tegminals have the spear-head end. The proximal end of the l. post. oro-tegminal is almost squeezed out of existence between the contiguous grooves. The r. post. oro-tegminal is transversely divided, and its proximal portion is nearly as large as the distal portion and swells out to almost the same width. The post. oro-tegminal is also divided transversely, and its distal portion is again split by meridional sutures into three elongate plates.

The Stem appears to have had a circular section, though in both A and B it is slightly crushed. The diameters in B are 5·2 mm. and 3·75 mm., giving a mean of 4·47 mm. The lumen in B has diameters *circa* 2·5 mm. and 1·75 mm., giving a mean of *circa* 1·9 mm.

The columnars are irregular plates, differing considerably in height and width, but tending apparently to form pentameres alternating about more or less radially disposed sutures. In the post. interradius of A the combined height of four such pentameres is 1·6 mm.; these alternate with three pentameres in r. post. IR having almost the same height. In the l. ant. IR of B the combined height of three pentameres is 2·7 mm., and in post. IR two pentameres have a combined height of 1·8 mm.

There seem to be traces of spine-pits on the pentameres.

Relations of *Steganoblastus*.

The meanings of all the structures that have just been objectively described will have to be discussed in a later paper. Here it is only the immediate conclusions that can be drawn.

First, the absence of brachioles, inferred from the lack of brachiole-facets and the presence of large cover-plates, proves that *Steganoblastus* is not a blastoid, not even one of the Protoblastoidea, as was at first supposed. It also proves, if proof be needed, that it is not one of the Cystidea Diploporita.

Secondly, the structure of the subvective groove, with its floor-plates and cover-plates, and its pores between the floor-plates, is paralleled by Edrioasteroidea alone among Pelmatozoa, and in that Class most closely by *Edrioaster*, though there are minor differences.

Thirdly, the presence of a stem, and the enhanced pentamerism of the thecal structures thereby induced, render it impossible to place *Steganoblastus* in the Family Edrioasteridæ. It has therefore been necessary to establish for it the Family Steganoblastidæ (*Treatise*, 1900, p. 209).

EXPLANATION OF PLATE XV.

Steganoblastus ottawaensis.

FIG. 1. Specimen A, from the posterior interradius, showing periproctals and, above them, the supposed hydropore.

,, 2. Specimen B, from the posterior interradius, showing the same features.

,, 3. Specimen A, the lip of the anterior subvective groove, showing pores, adradial suture, and spine-pits. For exigencies of lighting, the perradius is sloped downwards from right to left. × 5 diam.

,, 4. Specimen A, from the right anterior interradius.

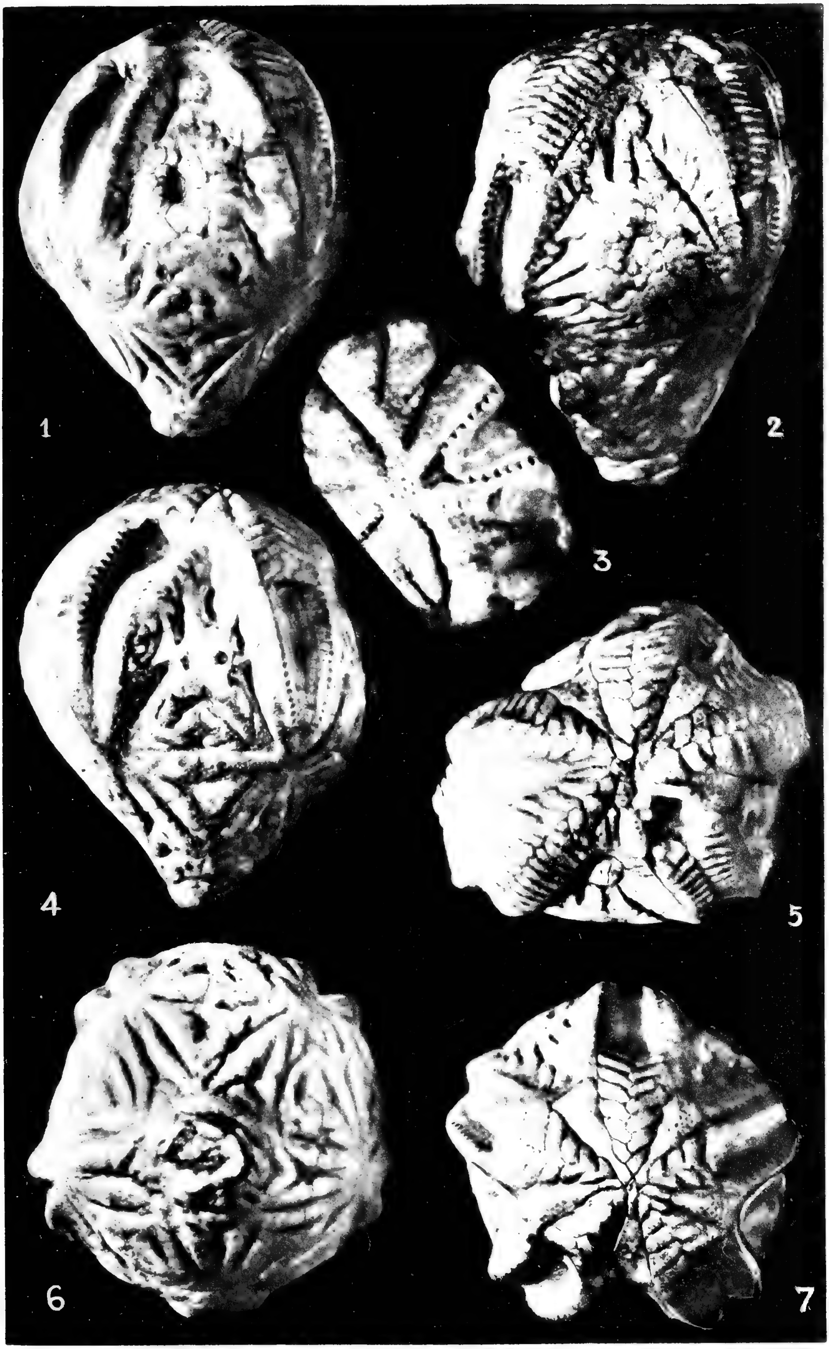
,, 5. Specimen B, adoral view ; compare Text-fig. 5.

,, 6. Specimen A, adapical view.

,, 7. Specimen A, adoral view ; compare Text-fig. 6.

All the figures are from photographs by Mr. H. G. Herring, and all, except Fig. 3, are enlarged 3 diameters.

The Text-figures are based on pencil drawings by Mr. G. T. Gwilliam.



Herring, photo. London Stereoscopic Co.

Steganoblastus.

VI. *Pyrgocystis* n.g.

[Part I.]

[Geol. Mag., n.s., Dec. VI, Vol. II, pp. 5–12, Pls. II, III: Jan., 1915.]

MATERIALS for the study of this very distinctive genus have been accumulating for many years, and at last afford a firm basis for certain definite conclusions. Some important matters remain obscure, and the comparison of the Swedish material has been hindered by the dangerous state of the North Sea, but further delay

in publication does not seem advisable. Various reasons make it convenient to deal with the species in the order of their geological age, beginning with the oldest, which is the most complete and is taken as the type-species of the genus. The new species are—

Pyrgocystis sardesoni, Lower Ordovician, Minnesota (genotype).
Pyrgocystis grayae, Upper Ordovician, Girvan.
Pyrgocystis ansticei, Middle Silurian, Shropshire.

To this genus are also referred some fossils from the Middle Silurian of Gotland which C. W. S. Aurivillius in 1892 regarded as representing seven species of the Cirripede genus *Scalpellum*. Though possibly to be reduced to only two species, they all appear to be distinct from the new species mentioned above.

The essential characters of the genus are displayed most clearly by the genotype *P. sardesoni*, to the description of which we now proceed.

A. *Pyrgocystis sardesoni* n.sp. (Plate II, Figs. 1–6.)

In March, 1901, Dr. F. W. Sardeson, of the University of Minnesota, himself a student of Palæozoic Pelmatozoa, was so generous as to send to me for study and description the rare and interesting fossils which give rise to this new genus, although he had originally intended to write on them himself. Not only this, but he has permitted me to retain the best specimen, returning him the others. Preliminary studies were made and drawings were prepared without undue delay, but various causes have up till now prevented the publication of the paper. This may seem a poor return for Dr. Sardeson's confidence, but the work at any rate has not suffered by keeping. It only remains for me to express my profound appreciation of his extraordinary kindness.

Horizon and Locality.—"The three specimens," says Dr. Sardeson, "compose all of the set, collected from the Ordovician Galena series, Stictopora bed; at St. Paul, Minnesota. The exact spot is a quarry on the west bluff of the Mississippi river, opposite the outlet at the east end of 'Pickerel Lake', as given on maps of St. Paul city."

The position of the Stictopora or, more correctly, Stictoporella bed in the Minnesota section is well known, but opinion as to the correlation with other regions has undergone much change The bed lies above the Platteville limestone and at the base of a series of shales successively termed Trenton, Black River, and Decorah, and now considered by E. O. Ulrich to represent the upper part of the Black River formation (see his "Revision of the Palæozoic Systems", Bull. Geol. Soc. Amer., vol. xxii, pl. 27; August, 1911). The Stictoporella bed comprises soft green shales and thin-bedded limestones, and is particularly rich in Polyzoa. According to R. S. Bassler (December, 1911, Bull. U.S. Nat. Mus., lxxvii, p. 38), the Decorah Shales correspond generally to the beds of Baltic Russia from the Wassalem beds (D 3) down to the Glauconite sandstone. But since the Kimmswick Limestone of Missouri (which corresponds to the top of the Decorah shales or even overlies them) contains a species of *Echinosphæra* said to be scarcely, if at all, distinguishable from

E. aurantium, it seems probable that the shales themselves correspond rather to the Orthoceras and Glauconite limestones which lie below the Echinosphæra limestone of N.W. Europe.

Material.—The three specimens may be denoted A, B, and C. A is taken as Holotype, and, having been so generously presented to the British Museum by Dr. Sardeson, is there registered as E 16,232. It was collected a few months before the other specimens, and probably came from a more exposed position, since it is partly weathered reddish-brown, whereas they are more grey. It is also rather better preserved, both as a whole and in detail, and the matrix has been more easily removed. B and C remain the property of Dr. Sardeson.

General Description.—A circular oral surface of general Edrioasteroid type, with (presumably five) straight broad subvective grooves, surmounts a cylindrical turret built up of scale-like plates imbricating from below upwards (i.e. adorally). The diameter of the turret is about two-thirds of its height. The scales bore spinules on their free borders; the oral face is obscured by longer movable spines.

Detailed Description.—The Oral Face is preserved well enough for description only in A, and here it is the perfectness of preservation that militates against description, since the greater part of the surface is covered by spines (Pl. II, Figs. 1, 2).

The diameter of the oral face is about 8 mm. Portions of four subvective grooves are visible; these are so situated that they appear to be on four adjacent rays out of a total of five; but which four they may be it is not easy to say. Two of the interradii, which are less covered with spines than the rest, are clearly neither of them the anal (posterior) interradius. Of the three remaining interradii, it is noteworthy that in one several of the spines, which seem to be a little longer, are directed towards a point at the margin of the oral face; and this suggests that the spines in question surround the anal opening. Taking this as a working hypothesis, for the present irrefutable, we find that the completely unexposed ray is the right posterior.

The Subvective Groove of the supposed anterior ray is seen to attain a width of 1·65 mm., and to be composed of a double series of plates, apparently alternating on the median line, and passing from that line outwards in a distal direction, so as to form an angle of about 140°. At the rounded distal extremity the angle becomes more acute, as the plates assume the usual fan-like arrangement. There are about five of these plates within a distance of 1 mm. An imaginary section across the whole structure shows the median line depressed, and the sides rising in a gentle convex curve, and then sinking again towards the outer edge of the ray or groove, so that this is clearly differentiated from the surrounding plates.

Of the right anterior groove, only a small portion is exposed, and this shows about five plates of one side all fenced round by spines. Each of these plates bears two tubercles, one on each brow of the convex curve, well raised above its general surface, and each depressed in its centre. It is natural to suppose that to each of these 'perforate' tubercles was articulated a spine, and this interpretation

is confirmed by the position of some of the neighbouring spines. Such tubercles were no doubt present on all the similar plates of this and of the other grooves, but of those other grooves it is only the left posterior which retains at all obvious traces of them; on the exposed portions of the remaining grooves they seem to have been less protected by preserved spines, and so to have been worn away.

The homologies of the alternating plates of the grooves are not quite certain. Presumably they must be either floor-plates or cover-plates. Since it is plain that they bore spines, they must have been, at least in part, on the exterior; and one would naturally infer that they were cover-plates. But they seem thicker and more curved and rounded than the cover-plates in Edrioasteridæ; and they might conceivably be floor-plates of which the elevated portions were exposed, leaving only the edges, especially near the median line, to be protected by small cover-plates now removed or unrecognizable. *Lebetodiscus* (Study III, December, 1908) presents such a structure, but in *L. dicksoni* the pores between the floor-plates are clear, whereas there is no trace of pores in *Pyrgocystis sardesoni.*

The Interradial Plates of the oral face are best exposed in the left anterior interradius, and to a less extent in the right anterior interradius. They merge into the imbricating plates of the turret, and the appearance is as though the turret-plates gradually became vertical and then inclined towards the oral centre. At the same time they become slightly thicker and much narrower, so that their relative thickness is considerably increased.

In part of the right anterior interradius and in the three other interradii these plates are obscured by Spines. Since these spines are of the same character as those on the grooves, it may be inferred that they were borne by similar tubercles. In the exposed interradii, however, such tubercles cannot be distinguished among the numerous irregularities of the surface. In the left posterior interradius some tubercles seem to be exposed, but it is difficult to distinguish between them and the ends of prostrate spines.

In the posterior interradius, as already stated, several spines, perhaps rather longer than most, are all directed in one way, and some of these converge to a point on the margin, to the right of the posterior interradius. A similar disposition of spines to protect the anal opening is common in spiniferous echinoderms.

The spines attained, in some cases at any rate, a length of not less than 1·3 mm. and a diameter of ·12 mm., tapering gently near the distal end. They show no sign of longitudinal striation, but are often irregularly blotched with black, which represents carbonized stroma and indicates a relatively wide-meshed stereom.

The Turret on which the oral face is supported has in specimen A (Pl. II, Fig. 4) a height of 13·2 mm., and it is uncertain whether the actual base is preserved; the cross-section is somewhat elliptical, with diameters of 10·8 mm. and 8·8 mm. In specimen B (Pl. II, Fig. 6), which seems to be still attached to a piece of rock, the height is 10 mm., and the diameters about 11 and 10 mm.; but here some of the adoral end may be missing. Specimen C (Pl. II, Fig. 3) has a height of about 11·5 mm., with diameters 10·8 and 8·2 mm.; and

here both ends may be incomplete. If allowance be made for imperfections and crushing, we may legitimately imagine a normal height of about 14 mm., and a diameter of 9·8 mm., or say two-thirds the height. The diameter seems to have been the same all the way up, and there is no indication that the turret was curved.

This turret is built up of a large number of separate thin plates, imbricating in such a way that their outer or free ends are directed upwards, i.e. towards the adoral face (Pl. II, Fig. 4). At the base of the turret these plates lie almost horizontally, but the inward dip gradually increases with each successive layer. The thickness of the turret wall is therefore at the base equal to the diameter of a plate; in A and C this amounts to at least 1·3 mm., leaving a lumen of about 7 mm. diameter (Pl. II, Fig. 3). Higher up the thickness does not decrease, but is formed rather by the combined thicknesses of the imbricating plates. The disc or body of the animal seems thus supported by the turret as a bird on its nest (Pl. II, Fig. 6). The arrangement of the imbricating plates is not very regular, but those of one tier tend to alternate with those of the tier below. In A the number of plates exposed along a single vertical line from top to bottom is about twenty-four; this means that the number of tiers is about forty-eight. About ten plates (twenty tiers) occur within 5 mm., but the plates are more widely separate above than they are below. Near the base four plates may be exposed along a vertical line of 1 mm., but this is in part due to the fact that the alternation is less regular, so that in these regions the number of tiers within the same distance would be only five or six, not eight. In the absence of a vertical section it is not possible to estimate precisely the proportion of each plate exposed, i.e. the extent of overlap; but the actual depth of the exposed portion in the upper part of the turret is about ·5 mm. It seems safe to say that not more than one-third of the plate is ever exposed.

No one of the turret plates can be entirely isolated, but in general outline those near the base may be compared to a salad-plate, with a slight concave curve next the lumen of the turret, and a stronger convex curve on the outside (Pl. II, Fig. 3). The convex curve is more pronounced in plates from the upper part of the turret. In specimen A a plate at the base has a width of about 3·75 mm. In other plates the width seems to have exceeded this, and to have about thrice the diameter. Probably the plates below are wider than those above.

Specimens A and C are laterally compressed, so that the cross-section of the turret may be said to have flat sides and rounded ends. Whether it bear any causal relation to this compression or no, it is the case that the tiers of turret-plates sink towards the base on the sides and rise towards the ends. This is visible at the very base in A.

In specimen C, which is generally of a yellowish-grey colour, the turret-plates are spotted with black in their stereom, and the spots are chiefly conspicuous on the free borders, where they seem rather regularly spaced. The meaning of these spots is suggested by A, for there, on the free borders of the turret-plates, are what appear to

be short spines, at fairly regular intervals of about ·2 mm., and each a little more than ·1 mm. long (Pl. II, Fig. 5). These spinules were, one supposes, attached to the turret-plates by strands of stroma, and it is the carbonized remains of the latter that form the black spots.

Diagnoses of the genus and of the species will follow the descriptions of the other species.

EXPLANATION OF PLATE II.

Pyrgocystis sardesoni.

FIG. 1. Specimen A. Oral face. The supposed anterior ray is uppermost; the bunch of spines supposed to be over the anal opening is near the lower margin, slightly to the right; above this on the right is exposed a part of the right anterior ray with tubercles. × 7·5 diam.

,, 2. Specimen A. Oral face. This photograph was taken before the specimen had been prepared quite so much as shown in Fig. 1. × 3 diam.

,, 3. Specimen C. Lower or distal end of turret, showing the large lumen. On the right the wall is bent inwards a little. × 3 diam.

,, 4. Specimen A. The turret from the supposed posterior side. × 3 diam.

,, 5. Specimen A. Part of the turret wall seen in Fig. 4, further enlarged to show the spinules. × 11 diam.

,, 6. Specimen B. The turret seen partly from above, showing how the centre is filled with plates. Portions of the shelly matrix still adhere to the sides of the turret, which is attached to a small fragment of rock. × 3 diam.

Figures 2, 4, and 5 are from photographs taken and worked up by Mr. Walter Moran. Figures 1, 3, and 6 are by the Author.

B. *Pyrgocystis grayae* n.sp. (Pl. III, Figs. 1, 2.)[1]

Material, Locality, and Horizon.—Among the echinoderms collected by Mrs. Robert Gray in the Starfish Bed of Thraive Glen, Girvan, is one, numbered by me K 8, which in general structure closely resembles Dr. Sardeson's fossil. The Starfish Bed lies near the summit of the Ordovician, as proved by the work of many geologists and palæontologists, whose remarks were summarized in my memoir on Caradocian Cystidea from Girvan (1913, Trans. R. Soc. Edin., vol. xlix, No. 6, §§ 6–8), where also the relationships of the Cystid fauna to those of other countries were discussed (§§ 559–568). Like all the fossils from the Starfish Bed described in that memoir, the present one is an imprint, and only one side is preserved.

General Description.—The differences between this, for the present, unique Girvan fossil and those from St. Paul lie mainly in the greater elongation and tapering of the turret and the elevation of the oral face into a high dome.

Detailed Description.—The oral face is mounted on a kind of Cup distinct from the stem or turret. This cup is formed apparently of thin imbricating plates, serially homologous with those of the turret, but higher and more closely united. At the top they are almost square-cut. In radial position they seem to bear no definite relation to either the rays of the oral face or the vertical rows of plates in the turret. Although these plates overlap at the sides, they all appear to

[1] Plate III, containing the figures of *Pyrgocystis grayae*, will be given with the second half of the paper in the February Number.

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London Stereoscopic Co., imp.

be of the same height and to reach approximately the same level. This height is about 1·3 mm. as measured from the top of the turret. The diameter of the cup at its upper margin is 4·7 mm., and below is about 3·8 mm.

The dome of the Oral Face reaches at its oral pole a height of 3·2 mm. above the cup, i.e. 4·5 mm. above the turret.

A single Subvective Groove faces the observer, and others are less clearly seen, one at each side. The groove attains a width of 1·7 mm., and is filled with alternating plates, which, as in *P. sardesoni*, may be either cover-plates or floor-plates. These plates are directed from the perradius outwards in a distal direction; the angle at which they meet is not easy to measure, but may be estimated at about 133°. The distal end of the groove is pressed against the plates of the cup, so that the arrangement of the terminal groove-plates cannot be made out. There are about three of these plates within a distance of 1 mm. A section across the groove-structures would show a broad convex curve sinking rather rapidly at each end towards the interradial area. The sutures between the groove-plates are depressed, especially along the median line of the groove, and appear rather irregular, as if they were either slightly crenelate and interlocking, or marked with alternating notches. There seems to be slight adoral imbrication of these plates.

Towards the oral pole the groove narrows considerably, and the curve of the cross-section is more markedly convex, almost angular. At the oral pole the groove-plates appear to meet those of the other rays, and there is no depression. That affords an argument for the plates being cover-plates.

The Interradial Plates of the oral face are hard to interpret. There seems to have been a single large plate within, and as it were continuing, the large overlapping plates of the cup. Then between this and the adoral groove-plates seems to be a single small plate.

The precise relation of these two interradial plates to the groove-plates is not easy to make out. There are appearances which remind one of the depressed sutures which in *Steganoblastus* continue the line of the sutures between the cover-plates. It might be inferred from this that the groove-plates, whether cover-plates or floor-plates, were in places separated from the larger interradial plates by small plates continuing the same line.

The surface of all the plates of the oral face is slightly rough, but it is not possible to say whether or no they bore spines.

The Turret is distinctly separated from the cup, at least in this unique specimen, owing to the fact that the cup-plates are more vertical, or in other words more parallel to the long axis of the animal, than are the uppermost turret-plates, and this divergence of angle results in a groove where they meet. It is, no doubt, conceivable that in other individuals, or even in this individual under other conditions of muscle-tone in life or of preservation in death, the uppermost turret-plates might be applied closely to the plates of the cup; but the distinction between cup and turret would be none the less decided, by reason of the less height of the turret-plates, or at any rate of their exposed portion. There is no reason

to suppose that the adoral region has been subjected to any such crushing or pulling as might have dragged it away from the rest. The turret then, for purposes of this description, is limited to the smaller plates, although in origin they must be of the same nature as the cup-plates.

The turret is clearly preserved for a distance of 13 mm. below the cup; beyond that distance, for 7 mm., the plates are much disturbed, but it is quite probable that the total height of the turret was 20 mm.

The diameter of the turret at its upper (proximal) end is 4·3 mm. Thence it tapers gradually, till at 13 mm. from the cup the diameter is 3·2 mm. Thus the mean diameter is about one-fifth of the height.

The turret is slightly curved.

The turret-plates imbricate adorally, and form a series of tiers. In the greater part of the turret the plates in one tier alternate quite regularly with those of the adjacent tiers. Thus the plates come to lie in definite vertical series or columns, those of one series alternating with those of the adjacent series. As the stem tapers distally the vertical series come closer together and the regular arrangement is lost. The distance between the tiers seems to become rather less as the proximal (upper) end of the turret is approached. In the upper half of the turret, i.e. in the proximal 10 mm., there are about 22 plates in vertical series, so that the usual amount of each plate exposed is about ·5 mm., a little less in the immediately proximal region, but scarcely ever more in the distal region. The number of tiers in the same distance is double, viz. 44; since there would be fewer in the distal region the total may be estimated at about 80. The number of vertical series visible in the proximal region is 5, from which a total of 10 at most may be inferred.

In spite of the regularity of tiers and columns, the wicker pattern produced is not very regular, and this is due to the ragged outline of the individual plates. Probably the adoral margin of each plate tended to form a convex curve; but the edge was thin and irregular, and has frequently been broken, so that the marginal curve is truncated.

It is quite possible that the free edge of the turret-plates supported minute spinules, but there is now no trace of such structures. At the very summit of the turret, however, lying against the outer cup-plates, are four vertical rod-like ridges; and these may represent spines.

VI. *Pyrgocystis* n.g.

[Part II.]

[Geol. Mag., n.s., Dec. VI, Vol. II, pp. 49–60; Feb., 1915.]

C. *Pyrgocystis ansticei* n.sp. and others. (Plate III, Figs. 3–15.)

Previous History.—In 1892 Professor Carl W. S. Aurivillius published his well-known paper "Ueber einige ober-silurische Cirripeden aus Gotland" (Bihang Svenska Vet.-Akad. Handl. Bd. 18, Afd. IV, No. 3). Besides the remarkable specimen from the Ludlovian *Pterygotus* bed of Wisby, to which he gave the name *Pollicipes signatus*, and a supposed fragment of a scutum, which he called *P. validus*, Professor Aurivillius described a number of "kurze, mehr oder weniger cylindrische, mit Schuppen bedeckte Bildungen", which he regarded as the peduncles of a cirripede and referred provisionally, in the absence of any trace of a capitulum, to *Scalpellum*. Though all the specimens (except possibly of *S. cylindricum*) came from a single stratum, bed *c* of Lindström, probably contemporaneous with our Wenlock Shale, and though the majority were found in a single locality, Djupvik in Eksta, still Professor Aurivillius considered that he could with certainty distinguish the following seven species:—

S. sulcatum,	p. 13, fig. 11,	Bed *c*,	Djupvik,	abundant.
S. varium,	p. 15, figs. 12–14,	,,	,,	1 specimen.
S. granulatum,	p. 16, figs. 20–22,	,,	,,	3 ,,
S. ,, ?	p. 17,	,,	Wisby,	some ,,
S. strobiloides,	p. 17, figs. 17–19,	,,	Mulde,	1 ,,
S. procerum,	p. 18, fig. 15,	,,	Wisby,	? ,,
S. ,,		,,	Djupvik,	? ,,
S. fragile,	p. 19, fig. 10,	,,	Djupvik, Wisby,	3 ,,
S. cylindricum,	p. 18, fig. 16,	(horizon not stated),	Wisby,	1 ,,

In 1906 Colonel [now] Sir J. Arthur Anstice, K.C.B., a son of the Mr. John Anstice of Madeley whose collection was mentioned by Murchison and Prestwich, presented to the British Museum various fossils from the Coalbrookdale district; and among them were 14 specimens of the same character as those described by Aurivillius, and like them coming from the Wenlock Shale. Consequently they were at first placed provisionally among the Cirripedia. When, however, Professor Moberg's recent memoir (1914) led us to look through our Palæozoic cirripedes, Mr. T. H. Withers directed my attention to these fossils. Immediately close examination under the lens revealed

at the broken edges of the plates the clean crystalline cleavage distinctive of calcite and of echinoderm stereom, but not found in fossil remains of Arthropoda. Their echinoderm nature once recognised, it is further clear that all these fossils represent the stems or turrets of species resembling those from Minnesota and Girvan so far as that portion of the anatomy is concerned, and probably resembling them in the structure of the oral face. It is interesting to note that among the Gotland fossils referred by Aurivillius to *Scalpellum sulcatum*, is one which Hisinger had previously figured as "Columnæ Crinoidis fragmentum" (1841, *Lethæa Suecica*, Supplementi Secundi Continuatio, pl. xli, fig. 6). This reference by Hisinger, which, bearing in mind the former extended connotation of the name Crinoidea, now proves perfectly correct, seems to have aroused no suspicions in the mind of Aurivillius. On the contrary, he was quite certain that these fossils represented the stems of some genus of Lepadidæ, and, despite the great extension of geological range involved and the absence of congeners earlier than Cretaceous, he scarcely hesitated to refer them to the characteristically recent genus *Scalpellum*.

Students of early Palæozoic fossils know how often it has proved difficult to decide whether isolated plates, or associated fragments, or even whole skeletons, belonged to the Echinoderma or to the Arthropoda; but the criterion of stereom-structure, when it can be applied, ought to prove decisive. Apart from that, in the present instance, Aurivillius himself notes that in the peduncles of Recent Cirripedia the scales are embedded in a thick [uncalcified] chitin, or are only fastened by the base. In other words, the peduncle-valves of the cirripedes are never so closely set or so deeply imbricate as are the plates in these Silurian fossils; and the consequence of this is that up to the present, as Mr. Withers assures me, only two specimens are known in which a scalpelliform peduncle has been preserved in the fossil state with its valves in place,[1] and not a single one has been found apart from its capitulum. What a contrast is provided by the fossils before us, of which over a score have been picked up on a single beach in Gotland and fourteen in one Shropshire lane!

But apart from these fairly obvious considerations, which would have made an ordinary palæontologist hesitate, the general shape of the individual plates might well have raised a doubt in the mind of so high an authority on the recent Crustacea as Professor Aurivillius. The peduncular valves of cirripedes always show growth-lines over the whole outer surface, and definite facets where they abut or overlap; they are clear-cut structures, and in *Scalpellum* at any rate the earlier the species the more characteristic is the shape of the plate. But the plates of these Wenlockian fossils show at the most some minute irregular granules or rugæ, and have no distinct ridges or facets; they are quite unlike any cirripede plates of either Silurian or Recent times.

[1] *Scillælepas carinata* (Phil.), Miocene, Sicily: Seguenza, 1876, Atti Accad. Pontaniana, vol. x, pl. viii, fig. 14; and *Pollicipes concinnus* Morris, Oxford Clay, England: Darwin, 1851, Pal. Soc. Monogr. Foss. Lepadidæ, p. 50, pl. iii, fig. 1.

Material.—The fourteen specimens presented to the British Museum by Sir Arthur Anstice are registered E 16233 to E 16246, but may for convenience of reference be denoted by the letters *a* to *n*. They are all turrets in various degrees of preservation. Specimen *c* [E 16235] is taken as holotype.

Horizon and Locality.—All are from the Wenlock Shale of Jig House Bank, or, in the local vernacular, "Jiggers Bank." This, says Sir A. Anstice *in litt.*, "is a road that runs from Coalbrookdale up the right hand side of a steep dingle called Lloyd Brook dingle (the main road from Coalbrookdale to Wellington runs up this hill) . . . the road runs up the side of a steep bank, and there is a place called the Loam or Lum hole in the lower part of the dingle."

Detailed Description.—These fossils closely resemble the "*Scalpellum sulcatum*" of Aurivillius, with whose description the following may be compared.

The Turret is slightly curved and increases gradually in diameter from below upwards, frequently expanding rather suddenly at its adoral end, where the plates appear more closely packed.

The plates are arranged in eight columns, which may (as in *c*, Pl. III, Fig. 4) be quite distinct with grooves between, but which may be partly merged so that it is hard to say whether the number is 7 or 8 (e.g. *a*, *b*, *f*, *k*; Pl. III, Fig. 3), or may be clearly not more than 7 (e.g. *d*, *e*; Pl. III, Fig. 5). The vertical seriation is most plain in the middle half of the turret; towards the adoral end there is nearly always an irregularity connected with the expansion of the turret, which is usually more on one side and affects the packing of the plates; towards the lower end, as the turret contracts, the columns inosculate and become reduced in number, so that there may be only 4 or 5 at the base, increasing to 7 or 8 above (e.g. *l*, *m*; Pl. III, Figs. 6, 10). When the irregularity of the upper expansion has come in before the increasing plates of the lower end have taken their positions in definite columns, then the arrangement appears quite irregular (e.g. *j*). In those regions of the turret, or in those individuals, in which the complete arrangement in eight distinct columns has not been attained, the inosculation of the plates frequently appears on the surface as a column of smaller plates between two columns of larger ones; one result is the absence of a groove between the columns and a more even rounding of the surface, as described by Aurivillius for his *S. varium* and *S. strobiloides*.

The shape of the visible portion of each plate varies with the extent to which it is exposed, and with the greater or less distinctness of the columns. The shape of the whole plate is given in Pl. III, Figs. 14, 15; and the only variation of this seems to be in the greater or less relative width, producing a more obtuse or more acute angle. The sides of the upper half of the plate form a somewhat parabolic curve, the whole of which may be exposed; but however little be exposed it can never be likened to the segment of a circle. In the lower half of the plate the sides become more straight and vertical, or even converge slightly. Of course it is only at the distal end of the turret that the plates are ever fully exposed, and it is probable that the

relative height is greater there. The measurements of such plates in millimetres are :—

	a	*c*	*e*	*j*
Height	2·9	1·8	2·75	2·7
Greatest width . . .	2·0	1·6	1·8	1·6
Depth of portion exposed .	·6	·4 or less	·5	·2 in column, 1·5 when alternating.

Thus the ratio of width to height varies from ·88 to ·59 in different individuals, when plates of the same character are compared.

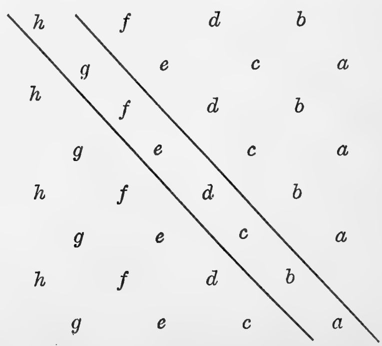
The number of plates in a column is 21 in *a* with a total height of 8·2 mm., 18 in *c* with a total height of 7 mm., about 16 in *e* where the portion preserved has a height of 5·6 mm., about 23 in *g*, with an approximate height of 8 mm. These numbers seem to imply that the plates are closer than in *S. sulcatum*, according to the measurement given by Aurivillius, who says 20 plates in 10 mm. But that measurement does not seem to take into account the more crowded plates at the two ends. His figure 11 suggests that there were in that specimen 27 plates in a height of about 10 mm. Probably there was no difference in this respect between individuals of the two species with clearly marked columns.

The amount of overlap is gauged by the proportion of depth of a plate exposed, and this in vertical series is somewhere about one-fifth. Aurivillius says of *S. sulcatum* "eine Schuppe nur die Hälfte oder oft nur $\frac{1}{3}$ der nächststehenden freilässt", but later on he gives the actual measurements for the middle region of the turret as ·5 in a length of 2·5 mm., i.e. one-fifth.

As regards the mutual relations of the plates in a tier, Aurivillius says: "Was die Anordnung in die Quere betrifft, stehen die Schuppen jeder zweiten Reihe auf derselben Höhe." If we letter the plates in a tier *a* to *h*, reading from right to left, then this sentence conveys the impression that the arrangement is as follows—

h *f* *d* *b*
g *e* *c* *a*

It will be observed that a repetition of this order in successive tiers would produce a line of the same letters ascending in spiral from right to left, *a* overlapping *b*, *b* overlapping *c*, and so on—



and a similar line descending from right to left, *b* overlapping *a*, and so on. This spiral arrangement is not conspicuous when the plates overlap closely, as in Aurivillius' fig. 11, and in those of our specimens that have clear vertical columns; but it is very plain when the overlap is less, though the alternation remains regular, as in Aurivillius' figs. 12, 15, 16, assigned by him to other species.

The slope of the plates towards the axis of the turret appears to be much as represented in Aurivillius' fig. 13, i.e. nearer the vertical below, and nearer the horizontal above.

In *c* the lumen at the lower end has diameters of 1·4 and 1·1 mm. The diameter of the turret at the top of the first tier of plates is 3·2 and 2·9 mm. (Pl. III, Fig. 8). This is the only specimen that shows a definite lumen at the distal end. In other cases the lumen is filled with plates (Pl. III, Fig. 7), or with plates and secondary calcite (Pl. III, Fig. 9), or it may be quite covered over with plates in a more horizontal position. Grinding down *n* at the distal end displays a section with diameters about 1·3 mm. and 2·9 mm. Aurivillius gives for *S. sulcatum* a lumen-diameter of barely 1 mm. and a turret-diameter [? same specimen and level] 3·5 mm. This indicates a relatively smaller lumen, but he says that the width increases towards the imagined capitulum. The section which he figures of *S. varium* (fig. 13) represents a different set of proportions; here the lumen does not increase upwards, but the contrary if anything, and at its lower end it is more than half the diameter of the turret, at its upper end a little less than one-third. In *S. strobiloides* the diameter of the lumen is said to be three times that of the wall; i.e. three-fifths the diameter of the turret. It is very doubtful whether the width of the lumen increased upwards in our Shropshire species; in the fossils at any rate it is filled with the more horizontally disposed and crowded plates, whose position cannot entirely be due to post-mortem shifting (Pl. III, Figs. 11, 12, 13).

The plates, when well preserved, are covered externally with fine anastomosing rugæ, showing a tendency to radiate towards the curved margins. Since these are developed equally on the exposed and unexposed portions of the plate, they must be regarded not as superficial ornament, but as an expression of stereom structure.

The plates are frequently broken on their free margins, so that either the tops are truncate or great pieces are, as it were, bitten out leaving jagged points conforming to the lines of crystalline cleavage (Pl. III, Fig. 3). This frequently gives the turret sides quite a peculiar appearance, as though they belonged to an entirely distinct species. The tops of the plates seem to be broken in the specimen of *S. strobiloides* shown in Aurivillius' fig. 17, which reminds one of the appearances in the Minnesota fossils.

There is no trace of any spines or spinules. But in *b* at the distal end, which is rounded, the ordinary large turret-plates seem to be covered by a number of very small plates the meaning of which is obscure.

Not a single specimen shows any trace of the oral face.

Measurements in millimetres are as follows:—

	a	*c*	*g*	*h*
Greatest length of turret	8·2	7	8·1	5·3
Diameter at adoral end .	4·0 × 4·4	4·9	5·1 × 5·7	2·2 × 3·5
Diameter at distal end .	ca. 3·0	3·2	ca. 3·6	1·5 × 2·8

Distinctions between the Wenlockian Species.—In spite of the variation as regards number and distinctness of vertical columns, there are good reasons for regarding all the Coalbrookdale specimens as belonging to a single species. First, the variations themselves merge into one another, and do so in such a way as to suggest that they represent stages of development, from fewer to more columns, and from alternation to seriation of plates. Secondly, there is little or no variation in the shape of the individual plates and in the nature of their ornament; and it is by characters such as these, little influenced by the cruder forces of the environment, that genetic differences are usually distinguished.

If now we apply the conclusions drawn from these Shropshire fossils to their contemporaries from Gotland, we find that the differences relied on by Aurivillius to distinguish his species are for the most part those which appear to us as simple growth-variations. So far as figures and descriptions allow one to judge, there seems no good reason why *S. sulcatum*, *S. varium*, and *S. fragile* should not all belong to a single species, for which the name *Pyrgocystis sulcata* would most naturally be adopted. *S. strobiloides*, represented only by the sole fragment found at Mulde, is probably no more than a slight variation, owing much of its different appearance to difference of preservation. *S. granulatum* seems to be distinguished by the nature of its ornament, but this again may only be due to better preservation; we have seen in *P. ansticei* that no weight can be attached to the difference in the direction of the plates at the distal end. Of the two long, cylindrical forms, *S. cylindricum*, known only from a single specimen, has plates of more pointed shape, and, since its horizon is possibly different, it may perhaps be left in its independence. The other, *S. procerum*, may also be distinct, but is more likely to consist merely of elongate individuals of *S. sulcatum*. It must be borne in mind that none of these specimens is really complete.

So much for the supposed differences between these Gotland forms. On the other hand, all, with the sole exception of the unique *S. cylindricum*, have plates of the same shape, namely, with the visible portion forming, in the words of Aurivillius, a segment of a circle. This fact, while confirming the view that they represent but a single species, sufficiently distinguishes them from the Shropshire specimens, in which the outline is consistently parabolic.

In the absence of any evidence to the contrary, such as might conceivably have been furnished by the oral face, these Wenlockian species must be referred to the genus *Pyrgocystis*.

The Relationships of Pyrgocystis.—It is clear that *Pyrgocystis* is an Edrioasteroid, but it is not clear whether it is to be referred to the Agelacrinidæ or the Edrioasteridæ. We need not consider either the Cyathocystidæ or the Steganoblastidæ in this connection.

According to the definitions given by me in 1899 and 1900 ("Treatise on Zoology," pp. 207–208), it would go more readily with the Agelacrinidæ; but in those definitions the differences in the subvective skeleton were not sufficiently taken into account.

In Studies I, II, IV, and V, the subvective skeleton of four Edrioasterid genera has been described in detail, and shown to consist of floor-plates and cover-plates, both disposed in alternating series, with pores between the floor-plates.

The evidence adduced by C. F. Roemer (1851), F. B. Meek (1873), Miller & Faber (1892), O. Jaekel (1899), J. M. Clarke (1901), and W. K. Spencer (1904) proves that in *Agelacrinus* (sensu lato) and *Hemicystis* among Agelacrinidæ, the subvective skeleton likewise consists of floor-plates and cover-plates, but that the floor-plates form a single series stretching right across the groove, and show no trace of pores. There is also a difference in the cover-plates, for normally in these two genera, as also in *Cystaster* and *Streptaster*, they are boot-shaped, with the sole of the boot adoral (= proximal) and the toe of the boot admedian, and in consequence of this shape they cannot close in the groove so completely as do the symmetrical cover-plates of the Edrioasteridæ. In some species of *Agelacrinus*, as shown in J. Hall's well-known figure of *A. cincinnatiensis* (1871), there are small additional cover-plates along the median line, much as may occur exceptionally in *Edrioaster* (Study IV, text-fig. 2). These additional plates, however, involve no departure from the essential plan of either group.

These two plans do not, I believe, exhaust the actual constructions employed in the Edrioasteroidea. Setting aside *Cyathocystis* and *Stromatocystis*, in which the structure is still not fully known, we may note *Lebetodiscus* (Study III), in which the cover-plates appear to be minute and to lie over the sutures between the floor-plates. The specimen figured by Jaekel (1899, *Stammesges. d. Pelmatoz.*, pl. ii, fig. 2) as *Agelacrinus Dicksoni* Billings, presents notches along the sides of its supposed cover-plates, and in other specimens I have observed these notches to be very distinct and regular: so that in such forms, it has seemed to me, there may have been minute cover-plates resting in the notches, and the larger visible plates may really be floor-plates.

The specimens of *Pyrgocystis*, so far as one can judge from the obscure evidence, do not display either cover-plates or floor-plates of the typical Edrioasterid or Agelacrinid plan. It is, however, conceivable that the plates observed correspond to the notched plates of the third plan of structure. Appearances that may possibly represent notches have been mentioned in the description of *P. grayæ*, and indications that the plates may perhaps not be cover-plates have been given in the description of *P. sardesoni*.

Those species which seem to me to have this supposed third plan of subvective structure, appear in all other points more closely allied to the Agelacrinidæ than to the Edrioasteridæ. In those same points it is with the Agelacrinidæ that *Pyrgocystis* also agrees. Therefore this genus may for the present be left in that Family. Although *Steganoblastus* is the genus of Edrioasteroidea that has the

most pronounced stem, and that manifests in its thecal structure the most pronounced reaction to such a mode of fixation, still it differs greatly from *Pyrgocystis* in the crinoid-like nature of that stem, in the solidity of the theca, and in the Edrioasterid character of the subvective skeleton. *Cyathocystis* again, especially in its more elongate individuals, presents a subvective system of straight grooves mounted on a turret of much the same proportions as in *P. sardesoni*. But the turret in *Cyathocystis* is a solid tube, and the structure of the whole oral face is totally different.

Among the Agelacrinidæ are some genera that approach *Pyrgocystis. Cystaster granulatus* as defined by J. Hall (October, 1871), from which Jaekel has attempted to separate some specimens as *Thecocystis sacculus* (1899), has straight rays surmounting an elevated sac-like body composed of minute plates or granules. In *Hemicystis* also the rays are straight, and Hall (October, 1871) specially mentions that *H. parasitica* and *H. stellata* have "the sides more abruptly elevated than the ordinary forms of *Agelacrinus*". The theca in *Hemicystis* is composed of minute squamiform plates. *Agelacrinus pileus* is said by Hall to have a "globular bell-shaped" theca when well preserved, and he figures a specimen in which many of the interradial plates "have a rounded node near the centre", possibly a spiniferous tubercle. In this species, as in all "*Agelacrinus*", the rays are curved.

The occurrence of spines in Pelmatozoa was probably more common than is generally supposed, but their preservation is certainly rare. Had specimen *a* of *P. sardesoni* not been found, nobody would have supposed that any species of *Pyrgocystis* bore spines; and the fact that they are not known in the other species is no proof that they were not present. No stress should be laid on the appearance of vertical rods on the cup-plates of *P. grayæ*, since they may be merely strengthening ridges. Meek (1873, Rep. Geol. Surv. Ohio, vol. i, pt. 2, p. 56) mentions ridges on the inner surface of marginal plates in an *Agelacrinus cincinnatiensis* (?).

Bionomics of Pyrgocystis.—The three formations from which specimens of this genus are known are of different lithological character.

P. sardesoni is found in a thin-bedded limestone, intercalated in soft green shales, and composed of numerous small fossils and fragments, but mainly of bryozoan skeletons, especially of branching bifoliate forms. This seems to suggest pure, relatively shallow water, crowded with animal life. The skeletons afforded a firm base of attachment for the Edrioasteroid's turret, which was under no necessity to be lofty since there was abundance of food and of aërating currents. There is no indication that the turret was fixed in other than a vertical position. The spines might conceivably be ascribed to some innate acanthogenous agency, or (less mystically) to an excess of lime in the water; but, whatever the contributory causes, we may suppose that the longer spines on the oral face were useful as a defence against worms and other predatory foes, while the spinules on the turret may have protected the soft stroma from parasitic organisms.

P. grayæ is preserved in a sandstone from which, as generally found, the calcareous constituents have been leached. This also was

a shallow-water formation, but not so rich in life as the Stictoporella bed, and especially poor in sedentary organisms. No firm base was afforded for the turret, which therefore seems to have tapered off to a pointed end thrust in the soft sand, while upwards it grew out of the reach of a bombardment by sand-grains (cf. "Caradocian Cystidea from Girvan", § 558). By the domed elevation of the oral face, the accumulation of sand-grains over the subvective system was prevented. The water was not so rich in lime, and parasitic enemies were not so numerous, wherefore it is probable that the reason why spines have not been preserved is because they never were developed in this species.

The Wenlock Shale of Shropshire, like the contemporaneous Bed *c* in Gotland, is a very fine-grained shale, apparently deposited in calm waters, in which lived a fairly numerous but rather dwarfed fauna, rich in ostracods and in small brachiopods and trilobites. There was no good fixation for the turrets, which seem therefore to have been rounded off at the distal end, and presumably stuck in the ooze, but may possibly have been attached to seaweeds. Frequently, it seems, they did not stand upright, and therefore grew in a slight curve. As a rule, relative want of lime made their plates thin and of a loose texture as now manifested in their dark colour. This also did not encourage the production of spines, which probably were absent. The differences between the various Wenlockian species do not seem to be of much physiological importance.

The results of the present Study may now be summarised in the following *Diagnoses*.

PYRGOCYSTIS[1] n.g.

An Agelacrinid with a subvective system of five broad straight rays mounted on a subcylindrical turret of adorally imbricate thin wide plates, which are not markedly different from those of the interradial areas of the oral face.

Range.—Lower Ordovician to Middle Silurian.

Genotype.—*P. sardesoni*.

P. SARDESONI n.sp.

A *Pyrgocystis* with diameter of turret equal all the way up, and about two-thirds its height, which is about 14 mm.; turret-plates in about 48 tiers of 11 plates in each, irregularly alternating and nowhere forming the complete 22 columns; each plate is from two to three times as wide as high, and is shaped like a segment of a flat ring. Not more than one-third of each plate is exposed. At the distal end of the turret the plates are almost horizontal; towards the proximal end they gradually approach the vertical, and finally merge into the interradial plates of the oral face, which is approximately horizontal. Spines are borne by all plates, those on the turret-plates being minute and not readily preserved.

Holotype.—Brit. Mus., Geol. Dept., E 16232.

[1] *πύργος*, a tower.

Horizon.—Stictoporella bed, Decorah shales, Lower Ordovician.
Locality.—St. Paul, Minnesota, U.S.A.

P. GRAYAE n.sp.

A *Pyrgocystis* with turret markedly tapering distalwards, its diameter in the proximal region about one-fifth its total height, which is about 20 mm.; turret-plates in about 80 tiers of about 5 plates in each, which in the proximal region alternate regularly so as to form about 10 columns; each plate appears to be probably wider than high, and to have an outer margin shaped like a flattened arc of a circle; the amount exposed is uncertain. The turret-plates seem to be laid at a steep pitch throughout; at the proximal end they form a distinct, almost vertical-walled, kind of cup, from which springs the high-domed oral face. Spines not observed.
Holotype.—Collection of Mrs. Robert Gray, Edinburgh, K 8.
Horizon.—Starfish bed, Drummuck series, Upper Ordovician.
Locality.—Thraive Glen, Girvan, Ayrshire, Scotland.

P. ANSTICEI n.sp.

A *Pyrgocystis* with turret slightly tapering distalwards, its diameter in the proximal region about one-half to two-thirds its total height, which is about 8 mm.; turret-plates in about 50 (or fewer) tiers of not more than 4 plates in each, which in the middle region alternate regularly, often forming 8 distinct columns separated by grooves; the width of each plate is from six-tenths to nine-tenths of its height; amount exposed about one-fifth, its margin a parabolic curve. The slope of the turret-plates in the fossils is nearer the vertical at the distal end, nearer the horizontal at the proximal end. Oral face and spines not observed.
Holotype.—Brit. Mus., Geol. Dept., E 16235.
Horizon.—Wenlock Shale, Middle Silurian.
Locality.—Jig House Bank near Coalbrookdale, Shropshire, England.

P. SULCATA Aurivillius sp.

Scalpellum sulcatum Auriv. 1892, p. 13.
Scalpellum varium Auriv. 1892, p. 15.
Scalpellum fragile Auriv. 1892, p. 19.
? *Scalpellum strobiloides* Auriv. 1892, p. 17.
? *Scalpellum granulatum* Auriv. 1892, p. 16.

A *Pyrgocystis* with turret slightly tapering distalwards, its diameter in the proximal region about half (or a little less) of its total height, which is about 11 mm.; turret-plates in about 50 (or fewer) tiers of not more than 4 plates in each, which alternate regularly, often forming 8 distinct columns, separated by grooves; the width of each plate appears [from Aurivillius' drawings; no measurements are given] to be greater than its height; amount exposed about one-fifth, its margin an arc of a circle. The slope of the turret-plates in the fossils is nearer the vertical towards the

distal end, nearer the horizontal at the proximal end, but they may be compressed and flattened at the extreme distal end. Oral face and spines not observed.

Holotype.—The original of Aurivillius' plate-fig. 11 is hereby selected. It is in the Riksmuseum, Stockholm. The holotype of *Scalpellum varium* is the unique original of Aurivillius' plate-fig. 12. The original of Aurivillius' plate-fig. 10 is hereby selected as holotype of *S. fragile*; it is not the specimen measured. The holotype of *S. strobiloides* is the unique original of Aurivillius' plate-fig. 17. The specimen measured by Aurivillius (p. 16) is hereby selected as holotype of *S. granulatum*; the figures may or may not be taken from this. All these specimens also are in the Riksmuseum, Stockholm.

Horizon.—Bed *c* (=Wenlock Shale), Middle Silurian.

Locality.—Djupvik in Eksta, also at Mulde and near Wisby, Gotland, Sweden.

P. procera Aurivillius sp.

Scalpellum procerum Auriv. 1892, p. 18.

A *Pyrgocystis* with turret almost cylindrical, its diameter in the proximal region about one-third of its total height, which is not less than 10 mm.; turret-plates in at least 25 tiers of 4 plates in each, which alternate regularly, forming 8 columns separated by faint grooves; the width of each plate appears to be greater than its height; amount exposed fully one-half, its margin an arc of a circle; each plate is slightly bent on its vertical axis. The slope of the turret-plates approaches the vertical in all the portion preserved. Oral face and spines not observed.

Holotype.—The original of Aurivillius' plate-fig. 15 is hereby selected; it appears to be the specimen measured (p. 18). It is in the Riksmuseum, Stockholm.

Horizon.—Bed *c* (=Wenlock Shale), Middle Silurian.

Locality.—Aurivillius gives *a*) near Wisby, *b*) Djupvik in Eksta. I do not know from which of these the holotype came.

P. cylindrica Aurivillius sp.

Scalpellum cylindricum Auriv. 1892, p. 18.

A *Pyrgocystis* with turret almost cylindrical, its diameter not more than one-third of its total height, which is not less than 9 mm.; turret-plates in at least 12 tiers of 4 plates in each, which alternate regularly, forming 8 columns, which are not separated but closely inosculate; the width of each plate is very little (if at all) greater than its height; amount exposed about two-thirds, its margin a pointed arch. The slope of the turret-plates approaches the vertical in all the portion preserved. Oral face and spines not observed.

Holotype.—The unique original of Aurivillius' plate-fig. 16, in the Riksmuseum, Stockholm.

Horizon.—Silurian, precise bed unknown.

Locality.—Near Wisby, Gotland, Sweden.

EXPLANATION OF PLATE III.

Pyrgocystis grayae.

FIG. 1. The holotype seen in three-quarter view from above, so as to show the oral face.

,, 2. The holotype seen from the side.

Both these figures are photographs from a squeeze of the original. × 3 diam.

Pyrgocystis ansticei.

,, 3. Specimen *a*. Side view. Note the irregular shape of the plates, due to fracture.

,, 4. Specimen *c*. Holotype, side view. Note the regular plates arranged in columns.

,, 5. Specimen *e*. Side view. Note the slightly irregular columns, of which there are only 7.

,, 6. Specimen *l*. Side view. Note the small number of columns at the distal end, with new ones coming in above.

,, 7. Specimen *g*. View of distal end. Since the turret is much curved, its side is also visible, though out of focus. There is no trace of a lumen.

,, 8. Specimen *c*. Holotype, view of distal end. The turret is slightly curved. There is a small distinct lumen.

,, 9. Specimen *e*. View of distal end. The position of the lumen is filled with a solid mass of plates and secondary mineral matter.

,, 10. Specimen *m*. Side view. Note the irregularity of the columns near the tapering distal end.

,, 11. Specimen *a*. View of adoral end. Note the approach to horizontality of the plates, and how they stretch across the lumen.

,, 12. Specimen *c*. Holotype, view of adoral end, as in Fig. 11.

,, 13. Specimen *i* [erroneously lettered *z* on the plate]. View of adoral end. Traces of the lumen are seen filled with matrix.

All the preceding figures, 3–13, are from photographs, taken and worked up by the author. × 3 diam., the same scale as Aurivillius' figures.

,, 14. Specimen *c*. Holotype. A plate at the distal end. × 7·5 diam.

,, 15. Specimen *j*. A plate at the distal end. × 7·5 diam.

Unfortunately it has not proved possible to obtain for comparison similar drawings of the plates in the Swedish species.

[**1915** 60]

VII. MORPHOLOGY AND BIONOMICS OF THE EDRIOASTERIDAE.

[PART I.]

[GEOL. MAG., N.S., Dec. VI, Vol. II, pp. 211–215; May, 1915.]

THERE have now been described all the known members of the Edrioasteridae and the very similar genus *Steganoblastus*, as well as a genus apparently connected with the Agelacrinidae but presenting some remarkable features, namely *Pyrgocystis*. It is proposed in this and the following Study to deal particularly with

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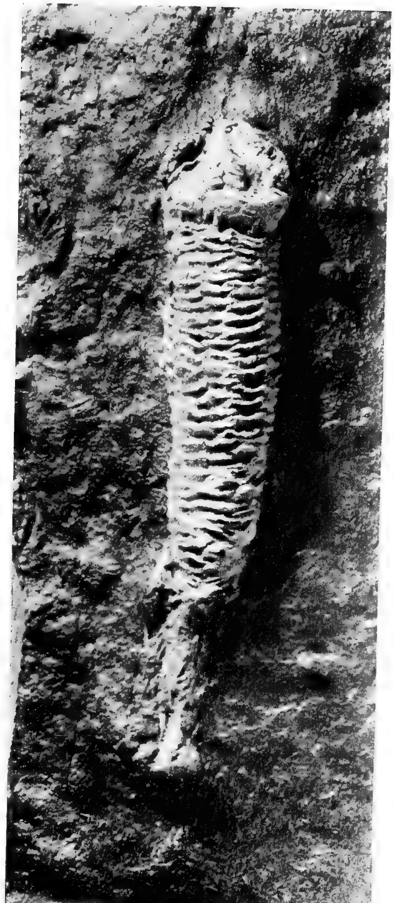

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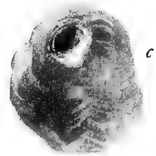

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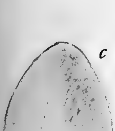

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London Stereoscopic Co., imp.

PYRGOCYSTIS GRAYAE, P. ANSTICEI.

the Edrioasterid organization, first considering what the known facts of skeletal structure imply as to the general anatomy and mode of life, secondly comparing the structure with that of other echinoderms, especially the Asteroidea. Although it may be necessary to refer to various facts that fall to be dealt with in future Studies, still the present seems a convenient opportunity for this general discussion, because of the recent publication by Mr. W. K. Spencer of the introduction to "A Monograph of the British Palæozoic Asterozoa" (Feb., 1914, Palæontogr. Soc. vol. for 1913), by Dr. J. F. Gemmill of his highly important memoirs on the starfishes *Solaster endeca* (1911, Proc. R. Phys. Soc. Edinburgh, vol. 18, pp. 174–91; and Feb., 1912, Trans. Zool. Soc. London, vol. 20, pp. 1–71, pls. i–v) and *Asterias rubens* (Oct., 1914, Phil. Trans., ser. B., vol. 205, pp. 213–94, pls. xviii–xxiv, and March, 1915, Proc. Zool. Soc. London, pp. 1–19, pls. i–iii), and by Dr. A. F. Foerste of some suggestive "Notes on Agelacrinidæ" (Sept., 1914, Bull. Sci. Lab. Denison Univ., vol. 17, pp. 399–486, pls. i–vi).

First, then, as to the internal organization and mode of life of the Edrioasteridae. It is clear from the position of the three openings—mouth, anus, and water-pore—on one face, that that face was directed upwards as in normal Pelmatozoa. Apart from that argument, the general resemblance of *Edrioaster* and *Dinocystis* to the undoubtedly sessile Agelacrinidae clearly indicates a similar position with regard to the sea-floor, even though the edrioasterids in question may not have been permanently attached. *Steganoblastus* obviously was fixed by a stem of ordinary pelmatozoan character, and by the mechanical stresses thus set up its theca has been modified so as to present a remarkable resemblance to that of a blastoid. How this stem originated is suggested by the parallel history of *Pyrgocystis*, in which we seem to trace the gradual elevation of the loosely and irregularly plated thecal wall, as seen in *Cystaster*, through the low turret of *P. sardesoni*, to the elongate stem-like turret of *P. grayae* and the more regularly plated turret of *P. ansticei* and *P. sulcata*.

Another criterion of Pelmatozoa is: "Food brought to the mouth by a subvective system of ciliated grooves, radiating from the mouth." The evidence for this in all Edrioasteroidea is the presence of radiating grooves protected by cover-plates, which plates are particularly well developed in Edrioasteridae and *Steganoblastus*, and apparently immovable over the mouth-region.

The only pelmatozoan character not yet mentioned is the presence of "an aborally placed motor nerve-centre". The presence of such a centre in *Steganoblastus* at any rate may be inferred from the stem with its lumen (Study V, 1914, p. 202) and from the axial folds similar to those which in many crinoids are known to have afforded passage for the nerves from that centre (Study V, p. 197). The possible relation of the lobes seen on the adapical face of *Edrioaster* to a chambered organ, such as that with which this nerve-centre is connected in the crinoids, was discussed in Study II (1900, p. 202). It is, however, scarcely necessary to point out that a sessile or almost sessile form such as *Edrioaster*, without stem and without movable arms, had little or no need for such a motor nerve-centre. If we

suppose the Edrioasteridae to be descended from forms with a more definite organ of attachment and with a moderately developed aboral nerve-system, we shall none the less expect to find that system considerably atrophied and leaving but slight traces. If, on the other hand, we suppose that the Edrioasteridae received their aboral nerve-system directly from the supposed anterior nerve-ganglion of some pre-echinodermal ancestor, *Dipleurula* or other, then again this will scarcely have been modified far in the direction of a motor centre. The same remark applies to any imaginable derivation of the Edrioasteridae from some echinoderm other than a Pelmatozoön, say a primitive Asterozoön.

The proof that the Edrioasteridae are Pelmatozoa in the full signification of that name has been laboured because the striking characteristic of this Family, more than of any other Edrioasteroidea, is just that strange resemblance to Asteroidea which suggested the second component of the Class name, and which will be fully discussed in the next Study.

Let us now consider more closely the Form and its relation to Fixation.

Edrioaster, *Lebetodiscus*, and *Dinocystis* have their rays curved like those of *Agelacrinus*, *Lepidodiscus*, and similar Agelacrinidae. This ensures a more or less circular outline of the theca or at all events checks any tendency to a star shape. That this curvature is secondary is an obvious conclusion from a comparison with the Agelacrinidae, from the facts of individual growth (Study IV, 1914, pp. 120, 121), and from the existence of the straight-rayed *Steganoblastus*. Further, the oldest known Edrioasteroid, *Stromatocystis* from the Middle Cambrian, has straight rays. This last form is pentagonal, with a tendency to be stellate; but it cannot therefore be inferred that its as yet unknown ancestor was more stellate. The assumption of a pentagonal or star shape is a consequence of the straight outgrowth of the food-grooves. All that we know of the evolution of those structures in the earlier Pelmatozoa indicates that, in race-history as in individual growth, they stretched gradually outwards from the mouth, and by degrees impressed a radiate symmetry on every part of the theca as well as on the internal organs. *Stromatocystis*, as will appear in a subsequent Study, affords no evidence of descent from an ancestor in which the radiate symmetry was more strongly marked than in itself. On the contrary, for this Cambrian genus, as for all the Ordovician Edrioasteroids, the natural inference is that they are descended from a simple sack-like, irregularly plated pelmatozoön with no more than the beginnings of radiation seen in its food-grooves, which at first were but three in number. (See Treatise on Zoology, 1900, p. 11; Study I, 1898, p. 545; Study V, 1914, p. 201; and A. Foerste, 1914, op. cit., p. 412.)

It is generally admitted that radiate symmetry of this kind can only have arisen in a fixed form, and that in the case of Pelmatozoa the fixation must have been by the apical end. Such fixation was retained, or perhaps emphasized, in *Cyathocystis* and *Steganoblastus*. *Stromatocystis*, however, the only Edrioasteroid as yet known from

Cambrian rocks, was certainly not fixed, and can have had at most a loose and variable attachment. Between these extremes lie all the forms of attachment found in the Edrioasteroidea, differing from genus to genus, and even from species to species, according to the needs of the environment. Thus, evidence has been adduced to show that, in spite of Jaekel's contrary opinion, *Edrioaster* and *Dinocystis* were not actually fixed (Study II, 1900, p. 200; Study IV, 1914, p. 169). Direct evidence is wanting in the case of *Dinocystis*, but the indirect proof is the same as for *Edrioaster*, namely, that the fossils are never found resting on any hard surface, but have the apical face covered with shale or sand, which cannot have afforded a firm basis of attachment. It is by parity of reasoning that *Pyrgocystis grayae* and its Wenlockian successors are supposed to have been not fixed but inserted in a sea-floor of similar loose consistency, although *P. sardesoni*, in its firmer surroundings, seems to have been fixed.

The general situation of such Agelacrinidae as '*Agelacrinus*' sensu lato, *Hemicystis*, and *Streptaster*, upon the smooth hard surfaces of shells and similar objects, suggests a permanent fixation, and I can recall no very clear evidence to the contrary. Dr. Foerste, however, says (1914, op. cit., p. 407): "In all of the Ordovician species referred to *Agelacrinus* or *Lepidodiscus*, the animal evidently was capable of attaching itself to various objects for support, although this attachment was not permanent, and occasional specimens are found unattached." The nature of this temporary attachment is imagined by Dr. Foerste to have been essentially the same as that suggested by me for *Edrioaster* and *Dinocystis*. As explained in Study II (1900, p. 202), it is supposed that this was effected by an action comparable to that of a limpet or a sea-anemone or of any mechanical sucker. In all the species of Edrioasteridae the necessary elements of the theca were present, namely an apical concavity, a rigid frame, and a central area of flexible integument. We know, it is true, nothing of the muscles within the thecal cavity that may have raised up this central integument, but the radial muscles of the flexible-tested sea-urchin *Asthenosoma* indicate how readily the necessary muscles may have been developed. Another mechanism, however, may be conceived. If, as here maintained, the pores between the floor-plates of the subvective grooves led from podia fringing the grooves to ampullae within the thecal cavity, then the distension of the ampullae by influx of water through the hydropore, or by retraction of the podia, would exert hydraulic pressure on the walls of the theca and their flexible portions would be inflated. If now, the ampullae were contracted and all their contained fluid forced into the podia or even out through the hydropore, then the flexible parts of the thecal wall would necessarily be drawn inwards. Thus, if the thecal margin were resting on a sandy bottom, a vacuum would be created, with consequent sucker action.

In so far as this latter hypothesis helps to account for the presence of pores in the free Edrioasteridae, just so far does it fail to harmonize with their presence in the fixed *Steganoblastus* with its more rigid theca. Moreover, if the Agelacrinidae were attached by sucker

action, their lack of pores prevents the extension of the hypothesis to them. It is, however, not only pores that are lacking, but also a plated apical integument, as may readily be proved by dissection or grinding either from above or from below, and by thin transverse sections (see further, W. K. Spencer, 1904, Proc. Roy. Soc., vol. 74, p. 43, l. 9, where for 'ventral' read 'dorsal'; also Foerste, 1914, op. cit., p. 409, § 13). Not that the absence of calcification would be the smallest bar to sucker-action, or to locomotion,[1] but it suggests that the animal rarely if ever relinquished its attachment.

The lobes of the flexible integument round the apical pole have been discussed more than once (Study II, 1900, p. 201; Study IV, 1914, p. 169). They have been found in all specimens of *Edrioaster* available for the prolonged preparation usually required; but this area is obscured in *Lebetodiscus*, and in *Dinocystis* all that can be traced is an occasional suggestion of an evagination (see text-fig. on p. 135, vol. 6, 1899) and foldings indicative of a stretched membrane (Study I, 1898, p. 546).

The number of lobes is five in the holotype of *Edrioaster buchianus*. In the specimens of *E. bigsbyi* the lobation is not so regular, but there are indications of the same pentamerism. Within the rounded margins of the lobes the integument is depressed, that is to say, withdrawn towards the interior of the theca. The lobes in *E. buchianus* were described as interradial, but in a form where the subvective grooves coil round from one radius into another, it is very difficult to decide upon the correct orientation of the apical face.

Whatever these lobes may mean, it is interesting to observe precisely similar structures, apparently with similar interradial position, figured by Jaekel in his *Thecocystis sacculus* (1899, pl. i, fig. 1 *b*) and described as an "Ansatzfläche" or "Anwachsungsfläche". In *Stromatocystis* also there is a pentagonal swelling with central depression round the apical pole, but the angles of the pentagon are prolonged in a distinctly radial direction.

This evagination may have had something to do with temporary fixation, but it does not reach as low down as the thecal periphery, and this function does not explain its quinquelobate structure. The only conclusions that can safely be drawn from the facts are that the shape indicates some rather firm internal organ or organs with quinque-radiate plan but without calcified skeleton. Beyond this all is pure speculation.

[1] Cf. G. H. Parker, "The Locomotion of Actinians": Science, March 26, 1915, p. 471.

VII. Morphology and Bionomics of the Edrioasteridae.

[Part II.]

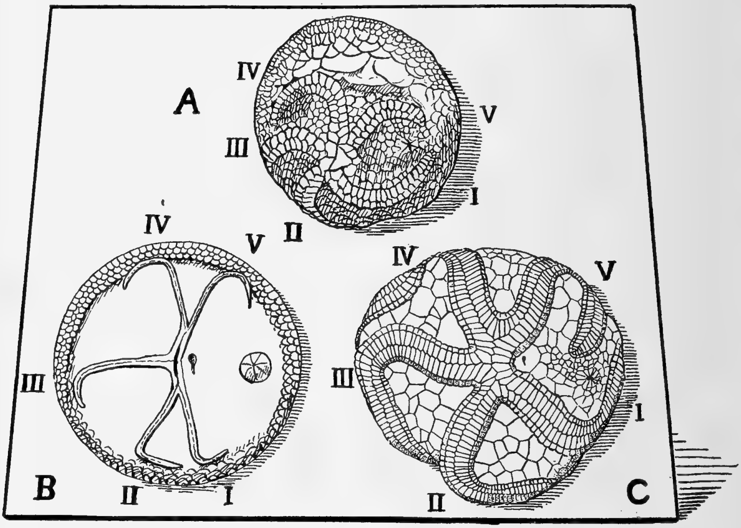
[Geol. Mag., n.s., Dec. VI, Vol. II, pp. 259–266; June, 1915.]

The facts concerning the Curvature of the Subvective Grooves have been summarized in Study IV (1914, p. 122). They show that no distinction can be drawn in this respect between Edrioasteroidea and Cystidea Diploporita, as some have pretended.

The facts of individual growth, as inferred from a comparison of large and small specimens of the same species, indicate that the rays increased in relative length with age, and thus wound more and more along the periphery. It may further be inferred, from tracing the course of each ray, that the initiation of the curve was due simply to the primitively straight course of the ray being turned aside by the peripheral limit. It follows from this that the right-handedness or left-handedness of the coil was not a feature of the young, and that the one is not a mere reversal or mirror-image of the other. The distinction, however, being characteristic of species separated by other characters, cannot be fortuitous. There must have been some structure or habit in each species predisposing a turn of the coil in a solar or contrasolar direction. It is clear that the cause cannot have been, as Jaekel seems to suggest (1899, p. 24), a torsion of the circumoral region, for in that event the proximal and distal curvatures of a single groove would never be opposed, as they so often are, and that not only in the right posterior ray.

If the difference of coil were due to such a fundamental change in the constitution of the animal as would produce a mirror-image, then the change would be accompanied by a change in the coil of the gut from solar to contrasolar or *vice versa.* This, however, does not seem to have been the case, for such evidence as we have as to the position of the rectum indicates a solar coil (as viewed from the oral pole) whether the grooves were solar as in *E. buchianus* (Study II, 1900, p. 199) or contrasolar as in *E. bigsbyi* (Study IV, 1914, p. 167). Jaekel's conclusion that the gut of the Edrioasteroidea had the normal solar coil of Echinoderma is probably correct, though his main argument, drawn from the supposed constant contrasolar curve of the rays, rests on an incorrect premiss.

A contrasolar curve of the rays, though not constant, is certainly prevalent in the Edrioasteroidea as a whole, and is regarded by Dr. A. F. Foerste (1914) "as the primitive condition among species with curved rays". Any explanation must, however, take into account the fact that it is so generally accompanied by a solar curve of the right posterior ray (V). To explain the latter feature, Dr. Foerste has put forward some plausible speculations, which if provided with a more extensive foundation of observed facts, might go far to solve the whole problem.



TEXT-FIGURE 1.—Diagrams to show the effect of a sloping position on the course of the rays.

A. A specimen of *Agelacrinus pileus*, traced from a photograph published by A. F. Foerste, 1914, op. cit., pl. ii, fig. 1. × 2 diam.

B. A diagram showing the effect of gravity on rays still marked by triradiate symmetry.

C. *Edrioaster bigsbyi* placed in the same position as A and B. Nat. size.

From observations mainly on *Agelacrinus pileus*, Dr. Foerste shows that the theca is frequently sagged to one side, and from this he infers the direction of slope of the surface (e.g. a valve of the brachiopod *Rafinesquina*) to which the Edrioasteroid was attached. If his argument be correct, then it appears that the right interradius (V/IV) was generally directed upwards, so that the anus was to the right of the mouth. Assuming, as is natural, that the slope of the brachiopod valve was toward the direction of the prevailing currents, then the anal stream would be swept away without passing over either the mouth or any considerable part of the food-grooves; moreover the greatest width of the peristome would be in the line of the current. So far, then, the interpretation of the facts is consistent with a healthy pelmatozoic mode of life. (Text-fig. 1, A.)

Dr. Foerste applies this probable position of the living animal to account for the reversed, i.e. solar, curve of the right posterior ray (V). Speaking of an Agelacrinid with its fixed border of small plates, he writes (p. 404): "the position . . . would tend to increase the tension along the upper part of the margin and just within the adjacent part of the peripheral ring. If, at the same time, the anus were dragged slightly downward and toward the left, the proximal part of the right ray (No. 4) being directed up the supporting slope, then the greatest tension would be on the upper, right-hand side of the inner curve of the peripheral ring, possibly sufficiently below the distal part of the right posterior ray (No. 5), in young specimens, to loosen the contact between this part of the peripheral ring and the immediately adjacent part of the posterior or anal interambulacral area, and thus to admit of the curvature of the right posterior ray in a solar, rather than a contrasolar direction." He finds support for this view in the frequent presence of small plates "along the upper margin of the anal pyramid", the animal being oriented as above described. However that may be, the presence of such small plates on the solar side of the anus (as already recorded in *Edrioaster bigsbyi*, 1914, Pl. X, Fig. 9), certainly indicates the presence of the underlying rectum, and thus confirms the view that the gut had a solar coil.

Dr. Foerste's argument has been given in his own words because it is not easy to follow. If, however, he is correct as to the normal position of the living animal, then we might find herein a very simple explanation not merely of the solar curve of ray V, but of the contrasolar curve of all the other rays. If the animal be laid on a slope with the anus to the right of the mouth, then its various parts are all subject to a gravitational force pulling down the slope (text-fig. 1, B). The grooves, with their cover-plates, their heavy floor-plates, and the various systems of organs associated therewith, are heavier, i.e. subject to a stronger pull, than are the intervening thinly plated areas. Consequently, when the grooves have grown out so far that they have to turn one way or the other, they will naturally turn in the direction of this pull. In other words, grooves IV, III, and II will acquire a contrasolar bend, and groove V a solar bend. Groove I should, on this hypothesis, most naturally have a solar bend; but owing to the greater width of the posterior interradius and the primitive triradiate plan of branching, the proximal position of this groove may very well have been directed almost straight down the slope, so that the action of gravity would be indifferent, and its course might rather be determined by the encroachment of groove II. The strong re-curvature of groove V is further aided by gravity acting on the rectum; but in forms that had structures such as ampullae on the inner side of the floor-plates, the posterior mesentery would have opposed an effective bar to the passage of the groove across it.

This hypothesis is suggested by facts observed in undoubtedly sessile forms, and if it is to be applied to the Edrioasteridae, we must suppose that they also assumed a similar sloping habit. Here, as in so many similar cases, the field collector and observers have not supplied the laboratory worker with the desired evidence. The section across a specimen of *Edrioaster bigsbyi* (1914, Plate X, Fig. 10) shows that,

in that individual at least, the right side was higher than the left. Let us, at any rate, test the hypothesis by applying it to the truly remarkable disposition of the grooves in that specimen (text-fig. 1, c). No sooner do we place the specimen on a slope, with the proximal region of ray IV directed upwards, than all the hitherto inexplicable curves appear the most obvious result of the downward pull. That peculiar inward bend of ray IV is a simple downward sag where its course is at right angles to the pull. The initial solar curves of rays III and IV, and the initial contrasolar curve of ray V, are similar sags, and contrast with the greater straightness of the corresponding region in rays I and II. Contrast again the sharp flexure of ray III, with the more rounded curve of ray II, and the still more open curve of ray I. At all points we see the action of the same force ; a force which may be slight but which is always at work. Now at last we appreciate the true meaning of what was previously styled the "peculiar aspect of independent life" given to these rays by their varying curves. There is here a struggle between two forces: the internal tendency of the grooves to grow straight outwards from the mouth at equal distances from one another, and the external pull of gravity, acting equally on all the grooves, but affecting each in a different way according to its position. Thus arises that unlikeness in likeness which gives the fossil its peculiar beauty.

If there be any truth in this explanation, it will of course be necessary to suppose that other species, with rays otherwise disposed, lived in a different position. In *Agelacrinus hamiltonensis*, for instance, ray IV must have lain more to the right, and so have come under the pull of gravity on that side with the result that rays I, II, III have a contrasolar bend, and rays IV and V a solar bend. In that species, with no internal ampullae, groove V has come right round the anus. It is not quite so easy to explain those forms in which all the grooves are either solar or contrasolar, but in the former it is worth noting that ray V is not strongly bent in towards the anus (see *E. buchianus*, 1900, Pl. VIII, and *E. levis*, 1914, Pl. XII); it would appear from this that the pull of gravity was, at any rate, not being exerted in the same direction as in *E. bigsbyi*. The greater width of interradius I–II in *E. buchianus* also suggests that its position was uppermost, so that the anus lay to the left of the mouth instead of to the right. In genera and species of later date, whether the flexure be solar or contrasolar, we must not expect to find such direct traces of mechanical causes. Those forms, we may most naturally presume, repeat the direction impressed on their ancestors when the conditions of life may have been different; they themselves may emphasize the direction by additional growth, as in the long lash-like grooves of *Dinocystis*, but they are not likely to change it.

Whatever truth there may be in the hypotheses here erected on the suggestive fact of position first recorded by Dr. Foerste, it does at least seem clear that all the differences may very well be due to simple mechanical causes acting on the growing animal. There is no need to invoke any sudden change of structure or constitution, any shuffling of chromosomes, or any reversal of development in early stages, as, for instance, by the splitting of the fertilized ovum into

dextral and sinistral halves. None the less, behind the simple mechanical explanation there still obtrudes the question: Why did one species place itself on a slope with its right side highest, and another species with some other side highest? Or if the external force was not gravity but the constant impact of a current, the question merely has to be posed in another form. There must be an answer to these questions, but we shall not discover it till we know the predecessors of these species, and perhaps not even then.

The Feeding of the Edrioasteroidea, as that of all other Pelmatozoa, was no doubt accomplished by the subvective system of ciliated grooves; but it does not follow that ciliary currents were the only means by which food was transported to the mouth. Reasons have been given for supposing that pores passed from the groove, between the floor-plates, to the thecal cavity in *Dinocystis* (1898, p. 545), in *Edrioaster buchianus* (1900, p. 196), in *E. bigsbyi* (1914, p. 124), and in *Steganoblastus* (1914, p. 198); and it has been argued, from the close similarity of the skeletal structures to those of an Asteroid, that there were external podia connected with internal ampullae. It is not supposed that these podia were provided with suckers, and without them they could not hand morsels of food along the grooves, or even assist the process in the way described by Dr. H. S. Jennings for *Asterias forreri* (1907, Pub. Univ. California, Zool., vol. iv, p. 93). They could, however, have performed some sweeping or pushing action, and may thus have contributed to the supply of food.

Respiration, it is probable, was the primary function of these podia. There is no sign of pores for papulae in any part of the thecal wall, so that these would have been the only extensions of thin-walled cavities available for the interchange of gases. The presence of a distinct hydropore confirms the view that the water-vascular system in these genera carried on some function of importance, whereas in Agelacrinidae the apparent absence of a hydropore is correlated with the absence of pores between the floor-plates.

The view that active podia existed in *Edrioaster* and its like, to which certain facts of structure point, is opposed by other facts of structure, namely, the completeness with which the cover-plates could close down over the grooves, and the position of the pores close up to the hinge-line of the cover-plates. The latter fact led Mr. W. K. Spencer (1904, p. 45) to cast doubt on the existence of podia, and to suppose that the pores had "a respiratory function", which means, apparently, that water was driven through them, by ciliary action (?), into some endothecal cavities not precisely indicated. Pores were supposed by him to be correlated with "firm skeletons", and to be absent from forms with "imbricating plates", which would "present large surfaces of membrane to the surrounding sea-water". This view, however, does not agree with the known facts; besides, the objection is not insuperable. Of course the cover-plates of *Edrioaster* were not closed when the animal was feeding, and it has already been suggested that they might open obliquely so as more readily to allow the podia to pass out between them (1914, p. 162). In the same place attention was directed to the possible openings immediately above the peripodium in *Edrioaster bigsbyi* effected by

accessory cover-plates. Were it not for these accessory plates (1914, p. 165, text-fig. 3) the supposition that the supra-oral cover-plates in that species were suturally united to form a solid tegmen would be inconsistent with the presence of pores all round the peristome.

The Food-grooves of *Edrioaster* and many other Edrioasteroidea are so distinct that they call to mind those structures in Cystidea Rhombifera that used to be called "recumbent arms". Those, however, are produced by the proliferation of circumoral plates over the outside of the theca. The resemblance is really closer to the epithecal grooves of the Diploporita. Their anatomical relations, and, in *E. levis,* their connection with the interambulacrals, show that the floor-plates are part of the thecal wall, not different in origin from the other thecal plates. As in the Diploporita we see to have been the case, so in Edrioasteroidea we may infer that the grooves passed out over the theca from the angles of the mouth, and that as they became deeper and more fixed, and as the cover-plates increased in size, so the subjacent plates became regularized. That is one possible hypothesis, and it seems to be the one held by Dr. Foerste (1914, p. 425). Another hypothesis is that the grooves passed out from the angles of the mouth between the thecal plates and not over them. This view is suggested by the appearances in *Stromatocystis,* and would have the advantage of making the floor-plates a double series from the outset. The disadvantage is the great weakening of the peristomial region which the hypothesis implies.

In any case a stage was reached sooner or later in which the ciliated grooves, with the underlying extensions of the nervous and water-vascular systems, passed over the floor-plates and under the cover-plates as in Diploporita. But from the Diploporita all Edrioasteroidea differ in the absence of exothecal projections (brachioles) bordering the grooves or forming the ends of their branches. From this point of view alone the Edrioasteroidea present an ambulacral structure divergent from that of all other Pelmatozoa, and this is why they have certainly better claims than the Blastoidea, for instance, to rank as a separate Class. In those Edrioasteroidea whose skeleton, like that of *Edrioaster*, bears witness to the presence of ampullae, this distinction is enhanced, not changed in character.

The structure of the Peristome has been described for *Edrioaster buchianus* (1900, p. 197, Pl. X, Fig. 2) and *E. bigsbyi* (1914, pp. 164–6, text-fig. 3, Pl. XIV, Fig. 2). It is clear that, as E. Billings noted in 1854, the gullet into which the food-grooves led passed into the stomach through a firmly-built ring or mouth-frame, of which the inner adcentral border turned down so as to form a rim, probably for the attachment of the stomach wall. As viewed from the oral aspect, after removal of all cover-plates, the chief elements of this frame appear to be five perradial plates, of which the exposed portions have a triangular outline. Viewed from the inside of the test, there are also seen to enter into this frame five interradial elements. In all the interradii except the posterior, and in all perradii, these elements appear to be formed of fused portions of floor-plates. In the posterior interradius there also enters into the

frame a portion of the large interradial plate that is pierced by the hydropore-canal.

In the Agelacrinidae an essentially similar peristomial frame has been described, first, obscurely by Miller & Faber in a specimen of *Agelacrinus pileus* (1892 Journ. Cincinnati Soc. Nat. Hist., vol. 15, p. 85, pl. i, fig. 10), secondly, in more intelligent detail from the same specimen, as well as in a specimen of *Streptaster septembrachiatus* by Dr. A. F. Foerste (1914, op. cit., p. 427, pl. i, fig. 5A, pl. ii, fig. 4, and p. 429, pl. i, fig. 7A, pl. iv, fig. 2), who has also favoured me with explanatory diagrams (in litt., 18 Feb., 1915). In the Agelacrinidae, as previously remarked (Study VI, 1915, p. 55) the floor-plates are quadrangular and stretch right across the groove; they may be composed of fused pairs of floor-plates of *Edrioaster* type, but direct evidence for this is lacking. The proximal floor-plate in each ray widens at its proximal or adcentral end, so that these five plates meet, except in the posterior interradius. The adcentral borders of these plates also bend down into the thecal cavity. Thus is formed a roughly circular or sub-pentagonal mouth-frame, similar to that of *Edrioaster* and confirming the interpretation of the radial elements in that genus as fused floor-plates. The gap left in the posterior interradius is filled in by one (*A. pileus*) or possibly more (*Streptaster*) of the posterior peristomial interradial plates, just as in *Edrioaster*. For minor details reference must be made to Dr. Foerste's account; but two structural features seem to have an important bearing.

In the specimen of *Streptaster*, when the mouth-frame is viewed from the inner face, there is seen on the left side of the posterior interradius a curved process, apparently attached to the inner face of the tegmen. This separates "a vertical cavity, less than a millimeter in diameter, apparently leading to the oral surface of the theca" just on the posterior side of ray V, from "a broad inclined groove" leading towards the thecal cavity between rays IV and V. Dr. Foerste's suggestion that this groove served for the passage of the gut seems entirely justified, and confirms the view that the gut had a solar coil. The stereom process served, one may suppose, for the attachment of one end of the posterior mesentery; and the deep narrow passage on the posterior side of it, adjoining ray V, was probably for the passage of a hydropore-canal. That, at any rate, is where such a structure would have lain if it existed.

In the specimen of *Agelacrinus pileus*, the posterior element of the mouth-frame is ridged on its inner face "somewhat like a letter W, the sides of the letter abutting against the thickened inner margins of the adjacent proximal floor-plates" of rays I and V. The middle ridge of the W passes towards the centre of the tegmen; and towards almost the same point are directed similar ridges on the inner faces of the tegminal plates between rays III & IV and III & II respectively. This suggests that the large posterior plate is a compound structure, consisting partly of an interradial element, partly of portions of original paired floor-plates, and partly of the cover-plates which have been transformed on the exterior into the posterior tegminal. Adjoining the margin of this plate where it abuts on ray V, and involving the two proximal cover-plates on the adanal side

of that ray, is "a peculiar margined depression". If, as Dr. Foerste suggests, "a duct passed by this path," then the duct in question would most naturally be the hydropore-canal.

The Relations of the Water-vascular System are of much morphological importance. The most natural interpretation of the appearances in the Edrioasteridae is that the perradial water-vessels lay at the bottom of the subvective grooves, on the ventral side of the abutting floor-plates, and that each gave off alternate branches to podia placed near the outer margin, and that each branch was also connected, through the pore between adjacent floor-plates, with an ampulla lying below (dorsal to) the subvective skeleton. This interpretation will be confirmed by comparison with a modern starfish. The perradial vessels passed to the peristome, and *Edrioaster buchianus* has already yielded evidence (Study II, 1900, p. 198) to show that they were there connected to form a hydrocircus surrounding the opening to the gullet, just above the mouth-frame. The hydropore lay in the posterior interradius, close to ray V, and passed through one or more interradial plates of the theca in a sloping direction from right to left. This direction indicates some torsion of the hydropore-canal and presumably also of the stone-canal, both of which must have been in the thecal cavity. Precisely where they became connected with the hydrocircus we cannot say, but it is plain that connection could readily have been effected by anyone of the ampullar or podial pores, and we may here recall that E. Billings observed a pore in the posterior angle to be larger than the others (Study IV, 1914, p. 164).

In the Agelacrinidae there is no such direct structural evidence for the position or even for the existence of perradial canals, not to mention podia. The shape of the cover-plates in most genera does, however, seem consistent with (one is tempted to say "calculated for") the extrusion of podia between them, and it seems natural to suppose that these structures were present, though unprovided with intra-thecal ampullae. An external hydropore has not as yet been detected, but it is conceivable that the hydrocircus opened into the oral vestibule, and that it may have been connected with some canal passing up in the posterior interradius (*vide supra*).

Edrioaster, *Agelacrinus*, and *Steganoblastus* present three modifications of an original subvective skeleton consisting of paired alternating floor-plates and cover-plates. In *Agelacrinus*, where ampullae were still unformed, the floor-plates became partly fused, but were still separated at intervals so as to maintain some flexibility. In *Edrioaster* the development of ampullae and more vigorous podia produced pores and combined with the general flexibility of the test to keep the original floor-plates distinct, except in the mouth-frame. In *Steganoblastus* the ampullae and podia remained, but the floor-plates fused and, in correlation with the rigidity of the theca, formed a single piece stretching right along under the groove.

VIII. A Comparison with the Structure of Asterozoa.

[Geol. Mag., n.s., Dec. VI, Vol. II, pp. 316–322; July, 1915.]

THE resemblance of the oral face of an Edrioasteroid to an Asteroid has not merely been remarked on by nearly every writer on the group, but has led many of them to far-reaching conclusions (e.g. Steinmann, 1888; Neumayr, 1889). None the less no exact comparison of the structures has yet been made; nor indeed was such possible until accurate descriptions were available. These have now been provided for various recent and fossil Asterozoa by many writers referred to in the sequel, and especially by Mr. W. K. Spencer (1914, "Monogr. Brit. Palæoz. Asterozoa"; Palæontogr. Soc.).

In general shape the Edrioasteroidea are more rounded and less stellate than the starfish. This is a natural consequence of the mode of life of the two classes. The Edrioasteroid that appears to have been the least sedentary, namely *Stromatocystis*, is also the most stellate. Similarly in Asteroidea the active Asteriidæ have, as a rule, longer arms than the more sluggish Asterinidæ and Echinasteridæ. Mere outline, then, has little genetic significance; the distinction, if any, lies in the large development of interambulacral plates in the Edrioasteroidea and their lack of marginalia, for the 'marginals' of *Agelacrinus* are scarcely homologous with those of Asteroidea. The observations of Mr. Spencer, however, "show that the most primitive Asterozoa have a leathery skin in which are imbedded small irregular plates" (p. 34), and that many of them "are devoid of differentiated marginalia" (p. 20). The specialization of the irregular plates into marginalia or other skeletal elements differed in the different branches of Asterozoa (Spencer, p. 8), just as it differed in the various genera of Edrioasteroidea. The ossicles of fundamental importance are those which were "the first to be laid down" or, at any rate, to be specialized from the indifferent coating of plates, namely, "those associated with the water-vascular system (ossicles of the ambulacral groove and mouth-frame)." It is to these, then, that our attention must be directed.

In the older Asterozoa, from which the true Asteroidea and Ophiuroidea were derived, the plates which in a modern starfish are known as "Ambulacralia" were "little more than mere flooring plates to the ambulacral grove" (Spencer, p. 21). They formed a double series, either opposed as in recent Asteroidea, or alternating as in *Edrioaster*. Spencer, following Gregory and Jaekel, regards the latter arrangement as the more primitive. These ambulacrals were approximately rectangular in plan, and excavated along the perradial sutures by a shallow "ambulacral channel" for the radial water-vessel. Along the sutures at right-angles to this the plates were deeply excavate, leaving a well-marked median transverse ridge along each. The longitudinal ridge, parallel to the ambulacral channel, was but slight, indicating the feeble development of the transverse ventral muscles.

Thus far the description is equally applicable to *Edrioaster*, but the difference from both *Edrioaster* and the true Asteroidea lies in the alleged absence of podial pores. It is presumed that branches led from the perradial water-vessel to podia placed somewhere in the depressions between the ridges; and it is possible that these depressions indicate the presence of incipient ampullæ; but, according to Mr. Spencer, the ampullæ had not yet penetrated to the interior. Were that view correct, *Edrioaster* itself would be more advanced in this respect than the older Palæozoic Asterozoa, and would find its analogue in such a form as the Lower Devonian *Xenaster*, where the pores have the same relative size and position (see Schöndorf, 1909, Palæontographica, vol. 56, pl. xi, fig. 2).

In reference to the earlier Asterozoa, Mr. Spencer says (p. 18): "Many investigators, owing to the poor state of preservation of their material, have described these depressions as pores for the

passage of ampullæ." This is probably true, and yet it does not follow that pores were not developed before Devonian time, or even that they were absent in the very cases to which Mr. Spencer refers. The true pores in *Xenaster* are difficult to see, by reason both of their position and their small size; they were probably even more difficult to see in the predecessors of *Xenaster.* Take *Lindstromaster*, for instance, from the Wenlockian of Gotland. Dr. J. W. Gregory, in his exceedingly succinct account (Geol. Mag., 1899, p. 347), said: "The ambulacral plates are boot-shaped. The pores for the podia are large." Apparently these statements were based on plates in which the depression was still partly filled by matrix. In other regions, however, the matrix has been most carefully removed, and the true structure is represented in Liljevall's accurate drawing (Geol. Mag., 1899, pl. xvi, fig. 1*b*, the ray in the south-east position, on the west and east sides of it respectively). The details are obscured in the half-tone reproduction, but I had the opportunity of comparing the original with the specimen itself in special reference to this point. The median ridges of the floor-plates run diagonally from the proximal adradial corner to the distal outer corner of each plate, so that, if the sutures be not carefully observed, the plates appear to be directed distalwards as they pass outwards. The sutures, however, really pass in the contrary direction. Thus the position where the pore should be looked for is where the suture meets the outer end of the ridge. Here the pore is indicated by Liljevall, almost hidden by the ridge and the overhanging "adambulacral", and here it does seem really to occur in the specimen, though proof by sections or grinding down is wanting.

If pores were absent in all the pre-Devonian Asterozoa, it would be very difficult to understand how the relatively narrow pores of *Xenaster* were formed. Starting with pressure of an incipient ampulla outside the floor-plates, one would expect to observe a gradual deepening of the excavation until it broke through into the thecal cavity as a relatively wide hole. Such is in fact the appearance presented by Professor Jaekel's drawing of *Siluraster perfectus*, from the uppermost Ordovician of Bohemia (November, 1903; Zeitschr. deutsch. Geol. Gesell., vol. 55, Protokoll. p. 108=p. 15). As our knowledge increases it may be that we shall find among the early Asterozoa, as among the Edrioasteroidea, some genera with podial pores, others without, forming parallel lines of descent. The presence of endothecal ampullae is necessarily dependent on the existence in the rays of a thecal cavity large enough to contain them.

The Cover-plates of *Edrioaster* appear to find their homologue in the so-called "Adambulacralia" of the starfish. These elements are thus described by Spencer in *Archaster typicus* (p. 13): "They are irregularly pentagonal in shape. The outer side runs almost parallel with the length of the groove. The face nearest to the groove has two facets [i.e. two sides of the pentagon]. The proximal facet is short and straight, the distal facet somewhat longer and slightly concave. We shall see that the appearance thus presented is characteristic of primitive Asterozoa and primitive Ophiuroidea as well as of the Asteroidea." This description applies almost exactly

to the cover-plates of *Edrioaster*, as may best be seen by a comparison with Text-figure 2 of Study IV (1914, p. 164). The difference lies in the greater development of articulating muscles and their surfaces of attachment in *Archaster*, especially in the fact that the adambulacrals are united to each other by a longitudinal muscle. It may also be noted that in *Archaster* each adambulacral is attached to two ambulacrals (floor-plates); Mr. Spencer, however, points out that the attachments are not really equal, as so frequently implied for this and other modern asteroids, but that one of the attachments preponderates and "connects the ambulacral to the adambulacral with which it corresponds in the series". In the early Palæozoic Asteroidea each ambulacral is associated only with its own adambulacral, just as in *Edrioaster* each floor-plate has its cover-plate. In these early forms also, as appears from the descriptions of Schöndorf, Hudson, and Spencer, the articulating sculpture and muscle-connections were much less developed.

The cover-plates of the Agelacrinidæ, recently so well described by Dr. Foerste (1914, §§ 16 and 22) are in some respects even more like Asteroid adambulacrals. The inequality of the admedian sides ('facets' W.K.S., *loc. cit.*) is generally exaggerated, so that in plan the visible portion of the cover-plate "has a spinous prolongation on the proximal side" (Foerste), or is "shaped like a bent finger" (Spencer, 1904), or is what J. W. Gregory calls 'boot-shaped', with the sole towards the mouth. Further, as Foerste has shown, in many of the Ordovician species the vertical section of a cover-plate is roughly sickle-shaped (or boomerang-shaped), the blade corresponding to the part which arches over the groove, and the handle to a narrower extension beneath the adjacent interambulacrals. Where blade and handle join is a slight groove between two ridges, forming an articulation with the floor-plate. Similar passage of the adambulacrals beneath the adjacent interambulacral (ventro-lateral) plates may be seen in many modern starfish. The chief difference is that the cover-plates of Agelacrinidæ are not one to each floor-plate; but this doubtless is due to the fusion of the floor-plates into groups, as already explained.

The adambulacrals of starfish do not close down over the groove in the same way as did the cover-plates of *Edrioaster*, and the contents of the groove are generally protected by groove-spines borne on the adradial margin of the adambulacral plates. None the less, by the approximation of the two sides of the groove, effected by the ventral cross-muscles, the adambulacrals may be brought quite close together, and in some species they may when thus closed be observed to alternate just like the cover-plates of an Edrioasteroid. See, for example, Ludwig, 1905, "Asteroidea of the Albatross," Mem. Mus. Comp. Zool. Harvard, vol. 33, fig. 51, *Pentagonaster ernesti*, fig. 135, *Paulia horrida*; Koehler, 1910, "Shallow-water Ast. Indian Mus.," pl. xi, fig. 3, *Pentaceros indicus*, pl. xii, fig. 2, *P. reinhardti*, and others; Gregory, 1899, op. cit. fig. 1*b*, *Lindstromaster*, the ray in the north-west position.

The alleged invariable presence of groove-spines, and the frequent presence of other spines on the adambulacrals of Asteroidea does not

constitute any serious difference. Spines were borne by the cover-plates in *Pyrgocystis sardesoni*, and reason has been given for supposing that they occurred in some other species of Edrioasteroidea. But since the cover-plates were in themselves sufficient protection for the grooves, there was not the same need for spines as arose in starfish with their more open grooves.

The Mouth-Frame of a modern starfish consists of five sets of paired radially placed elements and five sets of paired interradially placed elements. The latter, known as the "mouth-angle plates", are continuous with the adambulacrals, and are generally considered to be serially homologous with them. At any rate, they probably contain adambulacral elements, even if they may have incorporated some other constituent. The radially placed elements are admittedly ambulacrals (floor-plates) slightly modified. Morphologically then all these elements belong to the skeleton of the radial grooves. There is, however, another element, the so-called 'odontophore', lying in each interradius and abutting on the mouth-angle plates; whatever its ultimate origin, it presents the appearance of an unpaired interradial element.

For the present purpose it is quite unnecessary to enter into the perennial discussion as to the precise homologies of all these plates in Recent Asteroidea and Ophiuroidea. Comparison need be made only with the early Palæozoic Asterozoa, and here the problem is much simpler.

As an example of a very primitive mouth-frame Mr. Spencer (1914, p. 30) takes the fossil which he names *Eoactis simplex*.[1] His drawing (pl. i, fig. 4) shows a simple series of ambulacrals and of adambulacrals. At the proximal end of the groove the ambulacrals diverge, and the series is there terminated on each side by a curved subtriangular plate, which Mr. Spencer designates "mouth-angle plate". It is, however, clear from his drawing, no less than from the specimen itself, that this plate continues the ambulacral series and not the adambulacral, and this is further emphasized by the fact that the depression for the first podium lies equally on this plate and on the adjacent ambulacral. Further examination of other interradii in the fossil shows that this ambulacral mouth-angle plate was actually overlaid by a paired adambulacral element, though only the empty space that might have been occupied by such a plate is shown in the drawing. It follows from this that the plates marked by Mr. Spencer as A_1 and Ad_1 were really A_2 and Ad_2, and that the true proximal ambulacral and its corresponding adambulacral had not yet fused to form a mouth-angle plate. The continuity of the mouth-angle plate with the ambulacral series is also well illustrated by Spencer's drawing of those parts in *Stenaster obtusus* (1914, p. 32, text-fig. 28).

Turn now to the "series of schemes of buccal armatures of Palæozoic Ophiurids", published by Professor and Miss Sollas (1912, Phil. Trans., vol. 202, p. 226), and to Spencer's figure of *Lapworthura*

[1] This specimen, now in the British Museum, regd. E 13154, was No. 657 of the G. H. Morton collection, and comes from the Lower Ludlow or Upper Wenlock Beds of Hafod, Llandovery.

(1914, pl. i, fig. 9), and Jaekel's diagram of *Eophiura*, *Palaeura*, and *Bohemura* (1903), and it will be seen that the older the form, the more obvious is the composition of the mouth-frame from a series of ambulacrals diverging and becoming overlapped by the corresponding adambulacrals.

Perhaps the most instructive figure in this respect is that of the mouth-angle of *Siluraster perfectus* from the Upper Ordovician of Bohemia (Jaekel, 1903, fig. 3). Here is seen a series of adambulacrals each articulated with its corresponding ambulacral. The proximal adambulacral is enlarged to form a "Mundeckstück", but beneath it is still the ambulacral, though correspondingly reduced in size.

It seems a legitimate inference that all these plans of mouth-frame have been derived from one just a little simpler than the simplest of them, namely, a plan in which the ambulacrals were continuous right round the angle from ray to ray, each accompanied by its adambulacral. At first, no doubt, they were undifferentiated, so that the particular numerals attached to them, either here or in later forms, have no profound significance. Such a simple plan is essentially that of *Edrioaster* (Study IV, 1914, p. 164, Pl. xiv, fig. 2), but here already there is a condensation of the interradially placed floor-plates into a mouth-angle plate, a divergence of the proximal floor-plates of the groove, and an overlap producing in oral aspect the deceptive appearance of distinct perradial elements. The chief point of difference from any primitive Asterozoön lies in the fact that the adambulacrals of *Edrioaster* are still serving their primitive function as cover-plates.

The structure of *Edrioaster* suggests that even the interradially placed odontophore may be not of true interradial or interambulacral origin, but derived from the outer fused portion of the interradially placed floor-plates. On the other hand it is not quite certain that in *Edrioaster* itself this portion may not be in part an interambulacral with which the floor-plates have fused.

The curiously close resemblance between the ambulacral and peristomial structures of an Edrioasterid and those of a primitive Asterozoön would be strange indeed if their modes of feeding had been as different as those usually connoted by the names Pelmatozöon and Asteroid. We have, however, seen reason to believe that *Edrioaster* and *Dinocystis* were not permanently fixed; whence it may be inferred that they possessed some slight power of independent locomotion, towards which movements of the peripheral podia may have contributed. The existence of well-developed podia (a fact that cannot reasonably be doubted) further renders it probable that those organs helped in the transport of the larger food-particles to the mouth. Some Asteroids, on the other hand, and even some Ophiuroids, can use their podia for the same purpose; and some of the less active and less rapacious Asteroids can, as Dr. Gemmill has lately proved, subsist in part, if not entirely, by ciliary nutrition (March, 1915, Proc. Zool. Soc., pp. 1–19). Though a predatory mode of life was assumed at least as early as Devonian times by some starfishes with well-developed mouth-frame, e.g. *Xenaster eucharis* (see J. M. Clarke, 1912, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 15,

pp. 115–18, pls. xiv–xvi), it is natural to suppose that the ciliary and podial method was that chiefly practised by those earlier Asterozoa in which the mouth-frame was still but slightly differentiated.

We have now reached this stage of our discussion: we have seen, on the one hand, that by the middle of the Ordovician Epoch certain Pelmatozoa had acquired a structure of the rays and of the peristome strangely like that of the Asteroidea; and, on the other hand, that the Asteroidea and, to a less extent, the Ophiuroidea, as they are traced back through the geological periods, approach more and more in the same respect to the structure of the Edrioasteridæ. The conclusion that suggests itself is obvious, but not necessarily correct. Many difficulties have to be smoothed away before a genetic filiation between the two groups can be maintained.

The statement, for instance, that Asteroidea occur in the Cambrian is frequently made, and is always quoted by those who regard the Starfish as a very primitive group, or who deny the possibility of their descent from a form similar to any Edrioasteroid. So long as the term Cambrian was extended to the summit of the Caradocian, the statement was admissible. Nowadays it is misleading. No Asterozoa are yet known below the Middle Ordovician; Edrioasteroidea are known from the Middle Cambrian, and typical Edrioasteridæ were contemporaries of the earliest known Starfish.

Other difficulties are presented by differences of structure and by certain features of the development. These will form the subject of the next Study.

IX. The Genetic Relations to other Echinoderms.

[Geol. Mag., n.s., Dec. VI, Vol. II, pp. 393–403; Sept., 1915.]

THE last Study brought out many resemblances between Edrioasteroidea and Asteroidea, much closer than have been recognized even by some who have suggested a derivation of the latter Class from the former. In the present Study it is proposed to inquire whether that hypothesis, or any similar hypothesis, is tenable.

Apart from all other considerations, it is clear that, if *Edrioaster* has in its subvective skeleton reached a stage of development higher than that of the older Palæozoic Asterozoa, then it cannot be regarded as the ancestor of these latter. Further, it is hardly conceivable that the earliest Asterozoa known to us were derived from a genus entirely contemporaneous with them. But the Middle Ordovician Edrioasteroidea had, we know, ancestors in the Cambrian, so that the group was probably in existence in Lower Cambrian times, if not before; and it is among those early forms that the ancestors of the Asterozoa must be sought by any who would support the hypothesis under examination. The descendants of those ancient Pelmatozoa exhibited considerable diversity in regard to locomotion, and we do actually find in the Edrioasteridæ forms that have assumed many Asteroid characters. Surely there may have been other descendants with a tendency to similar structures, but adopting a mode of life in which those structures found larger scope for exercise and development. We know, it is true, that similarity of form is in itself insufficient evidence of blood-relationship; and yet there may be something in Mr. Bergson's argument that the independent appearance of similar structures in different groups points to some identity of initial impulse impressed on a common ancestry.

Time-relations, then, admit the possible derivation of Asterozoa from Edrioasteroidea. But of the three main changes involved in such derivation we have as yet only considered two, namely, the change of function in the ambulacra from nutrient to locomotor, and the elaboration of the mouth from a passive funnel to an active predatory organ. These two changes involve no difficulty, but the third, on which they both depend, is less easy to explain. It is the reversal of the main axis of the body with reference to the substratum; in other words, the transference of the oral pole to the under surface.

In a Pelmatozoön the main axis is vertical, the oral pole is uppermost, and around it are the water-ring (from which proceed the perradial canals), the hydropore, the genital aperture (when present), and the anus; the coil of the gut, when viewed from the oral surface, is dextral or solar. In a primitive Holothurian the main axis is horizontal, the oral pole is anterior, and around it are all the above-mentioned organs except the anus, which is posterior; the coil of the gut is the same. In a regular Echinoid the main axis is vertical, the oral pole is lowermost, and around it is the water-ring, from

which proceed the perradial canals; the hydropore, the genital apertures, and the anus are at the apical pole; the coil of the gut is the same. The orientation of an Asteroid is essentially the same, except that the genital apertures are marginal, and that the gut is not obviously coiled; the relative positions of the anus, when present, and of the madreporite are, however, in accordance with a solar coil (see *Treatise*, 1900, pp. 21 and 34), and such a coil does appear in early stages of development (Gemmill, 1914). An Ophiuroid differs from an Asteroid in the entire absence of anus, and in the position of the hydropore on the oral surface.

Therefore, the passage from a pelmatozoan to an echinoid or asteroid type involves: (1) the translation of the mouth, the water-ring, and the proximal ends of the perradial water-vessels, from an upper to an under position; (2) the translation of the hydropore, the anus, and, to a less extent, the genital apertures, from the oral to the apical surface; (3) the retention of the solar coil of the gut when viewed from the oral surface. Two modes of effecting the passage are conceivable. The first demands (*a*) the closure of the original mouth and the breaking out of a new one at the opposite pole; (*b*) the corresponding sinking of the circumœsophageal water-ring and the evolution of an entirely fresh set of perradial water-vessels starting from this new oral pole; (*c*) the reversal of the coil of the gut; it does not demand any essential alteration in the position of anus, madreporite, or genital apertures, or in the normal position of the theca as a whole. The second mode demands (*a*) the turning upside-down of the whole theca; (*b*) the migration of hydropore and anus along the posterior interradius towards the aboral pole, and, as a consequence, the elongation of the stone-canal; (*c*) a change in position of the genital apertures; it does not demand any alteration in the original mouth, in the coil of the gut, or in the other relations of the water-vascular system. The position of the genital apertures may be neglected, for in either case there must have been an entirely independent evolution of pentamerism in the gonads, and probably the bursting through of a fresh set of apertures. However this may be, there is little doubt but that the second mode of passage is the more in accordance with general echinoderm evolution. The migration of the hydropore may be paralleled in holothurians, and the migration of the anus in crinoids and echinoids. There remains only the initial step—the overturning of the whole theca.

It is clear that a change of this magnitude was no sudden one. As Professor MacBride has happily remarked, "No animal ever went to bed with one set of habits and woke up in the morning with another." In the absence of direct evidence we can only speculate, but our speculations must be controlled by two distinct sets of facts and principles. The changes imagined must be consistent, first, with the ordinary processes of life and the general character of such changes in the Echinoderma, secondly, with the facts of development in the recent Echinoderma concerned.

A possible mode of origin of Asterozoa from some early Edrioasteroid has been suggested briefly in the *Encyclopædia Britannica*, Supplement, vol. 27, p. 623 (July, 1902) and Eleventh Edition, vol. 8, p. 877

(Feb., 1911), and more fully expressed in "What is an Echinoderm?" (Journ. London Coll. Sci. Soc., vol. 8, pp. 21–33, May, 1901; Italian edition, Oct., 1901). This hypothesis has been criticized on the ground of the structure of certain fossils by Mr. W. K. Spencer (1904), who, however, now recognizes that he "overstated" his "case . . . It is not difficult to imagine a more primitive Edrioasteroid which would show, at any rate, near relationships with the ancestral Eleutherozoa" (1914, p. 6). More weighty objections have been raised by Professor MacBride and Dr. Gemmill on the ground of their admirable observations on Asteroid embryology. But while the hypothesis which they themselves adopt, as expressed in Professor MacBride's *Textbook of Embryology: Invertebrata* (1914, pp. 560–5), is difficult of acceptance, on the other hand some of their own recent observations seem actually to support the hypothesis which they reject. Let us consider these conflicting views more closely.

We now agree on many points of fundamental importance. We agree, namely, that the ancestral Asterozoa were attached by a stem homologous with that of the Crinoidea in so far as it was derived from the same portion of the larva. We agree that the ancestral Asterozoa fed by a subvective system of ciliated grooves. We agree that radiate symmetry was—in Eleutherozoa as in Pelmatozoa—a consequence of this mode of life. It is admitted that processes subsequent to the fixation of the bilaterally symmetrical ancestor by its anterior end eventually brought the stem: (*a*) in Crinoidea, to an aboral position outside the water-ring; (*b*) in Asterozoa, to an excentric oral position within the water-ring. We even appear to be agreed as to the changes that produced the plan (*a*).

The difference arises with regard to the number and order of the steps that produced the plan (*b*).

Whereas some of us have expressed the opinion that the ancestors of the Eleutherozoa passed through a true pelmatozoan stage, with mouth uppermost, and that to this stage the Echinoderma owe their coiled gut and radiate symmetry, MacBride and Gemmill hold that "the Echinoderm stock became split into two stems" shortly after the ancestral Dipleurula had become fixed by its prae-oral lobe, and after the organs of its left side had begun to grow more rapidly than those on the right, but "before the hydrocoel was a closed ring, and before radial symmetry was completely attained". From such a stage, they maintain, the primitive Asterozoön evolved immediately and directly, with its mouth turned towards the sea-floor, so that the left hydrocoel, as it developed into a hydrocircus, grew round the stem, which was therefore on the oral face; and it was while the creature was so supported that radial symmetry was acquired. Figures illustrating this view are given in MacBride's classical paper on "The Development of *Asterina gibbosa*" (1896, Quart. Journ. Micro. Sci., vol. 38, pl. 29, figs. 157–9) and are reproduced in his *Textbook of Embryology* (1914, p. 563). It should be noted that in the *Cambridge Natural History* (1906, Echinodermata, p. 621) a mistake crept into the diagram of the primitive Pelmatozoön, in that the gut was given a contrasolar coil.

It is, presumably, the position of the stalk within the hydrocircus,

as observed in the larva of the modern Asteroid, that forms the basis both of MacBride's own hypothesis and of his criticism of the so-called Pelmatozoic Theory. It may, however, be pointed out that in the history of both the Echinoderm race and the Asteroid individual, the hydrocircus begins as a hydrocoel crescent; also that in the larval Asteroid the stalk is on that side of the mouth where the crescent is open, and is not within the circumoral nerve-ring. The passage of the stalk in either direction would therefore be quite easy at a far later period of race-history than that to which Professor MacBride feels compelled to restrict it.

Now the two remarkable features of Echinoderm morphology which any hypothesis should seek to explain are, first, the hypertrophy of the left side with the correlated torsion, secondly, the radiate (normally quinqueradiate) symmetry.

The first of these, which affords the chief reason for the Pelmatozoic Theory, is frankly left unexplained by Professor MacBride. He writes: "It can only be described as an idiosyncrasy of Echinoderms that bilateral symmetry is unstable, and that, therefore, radial symmetry was arrived at by the overgrowth of the organs of the left side, etc." (1914, *Embryology*, p. 562). Similarly Professor Hérouard in an interesting note (Jan., 1915, Bull. Inst. Océanogr. No. 301) describes this "idiosyncrasy" as a hemiplegia, "un phénomène tératologique . . . dont nous constatons l'apparition sans malheureusement pouvoir en expliquer les causes." "On peut dire, que la série des ètres [échinodermales] que nous considérons comme représentant l'évolution normale, n'est dans sa totalité qu'une branche de la tératologie représentant la série des monstres nés viables et capables de se reproduire."

On the supposition that the tendency to this monstrous paralysis of the right side arises from something in the larva itself, the only explanation hitherto suggested has been that of Dr. Fr. Meves (1912, Arch. mikr. Anat., vol. 80, pp. 81–123). Having observed in *Parechinus miliaris* that the middle-piece of the spermatozoön passes at the first cleavage of the spermovum into one of the two blastomeres, he supposes that the substance of the middle-piece is, in the course of successive cleavages, eventually confined to that part of the pluteus which becomes the sea-urchin, and that those parts of the pluteus which disappear consist of cells which, in the course of cleavage, have received none of the middle-piece substance. This hypothesis is merely a succession of uncorroborated assumptions, and even if we could for a moment accept the supposition that the male characters (Vererbungspotenzen) were confined to the embryonic echinoderm, the remaining cells of the larva being merely trophoblast, we should not thereby explain the peculiar changes of symmetry.

Reducing it to its simplest terms, Hérouard (1915) describes the change as the replacement of the original binary axis by a secondary quinary axis. In Asteroidea and Echinoidea, he says, this quinary axis is at right angles to the binary axis. In Ophiuroidea and Holothurioidea, which both MacBride and Hérouard regard as derived respectively from Asteroidea and Echinoidea, the quinary axis is inclined to the binary axis and ends by almost coinciding therewith.

In Pelmatozoa also the quinary axis comes almost to coincide with the binary axis, but its direction is reversed.

Of these changes the Pelmatozoic Theory offers an explanation which, whether correct or no, is at any rate less transcendental than appeals to "idiosyncrasy", invisible "Vererbungspotenzen", or "hémiplexie tératologique". By this theory the relations of the axes of symmetry emphasized by Hérouard are interpreted in accordance with the life-history. The Dipleurula becoming fixed by its anterior end, the mouth passes to the opposite pole, and thus arise the Pelmatozoa with axis vertical and in a reversed direction to that of the Dipleurula. The change from these to the earlier Eleutherozoa is complicated by the retention of the stalk; the whole oral surface bends over, and the quinary axis is at right angles to that of the Dipleurula. In the later Eleutherozoa the process is carried further, and the quinary axis returns almost to the position of the original binary axis.

The associated changes in the torsion of the gut and in the movements of the coelomic cavities, loosely moored in the body-fluids, are described in the *Treatise on Zoology* (1900), and in the writings previously referred to (1901, 1902, 1911). We pass them by for the moment to consider the second morphological feature, the radiate symmetry.

Radiate symmetry arises and is maintained when an organism is evenly related to its environment on all sides. This happens in the case of fixed organisms, when they gather their food from all quarters irrespectively, by leaves or by tentacles or by ciliated grooves; in the case of free organisms, when they move indifferently in the direction of any radius. This evenness of relation may be interfered with from without or from within: from without, especially in the case of a fixed organism, when the situation is such that currents of air or water, or rays of light, beat on it mainly from one side; from within, by some change in the organism itself whereby its relation to the environment is altered, as when a free organism takes to moving in the direction of a particular radius (cephalization), or when a fixed organism for some special purpose (e.g. excretion) enlarges one of its unpaired asymmetrically situate organs. The Echinoderma, which, even in the most specialized Ophiuroid, never have attained an absolute radiate symmetry, present us with examples of almost every conceivable departure from such symmetry in forms both free and fixed.

Now Messrs. Gemmill and MacBride fully accept these views as to the origin of radiate symmetry, and believe with me that the free Echinoderms owe the radiate arrangement of their organs to inheritance from a fixed ancestor, which acquired that arrangement in consequence of the radiate extension of its food-catching organs. But the mode of fixation which they postulate, namely by a stalk asymmetrically placed on the oral face, is not one calculated to lead to such symmetry. Not merely does it appear exceedingly improbable that an animal feeding solely by ciliated grooves should ever have assumed or maintained such a position, but even if it did so it would not have been evenly related to the environment on all sides. In those Pelmatozoa that have assumed a similar position with reference to

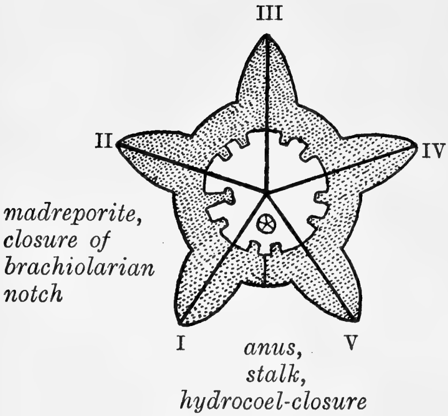


FIG. 1.

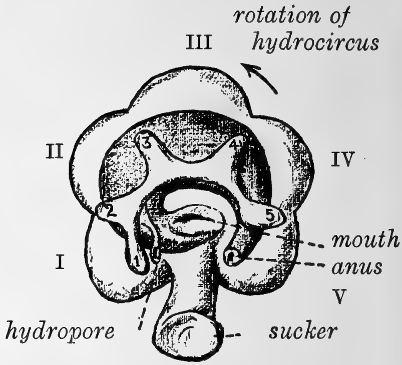


FIG. 2.

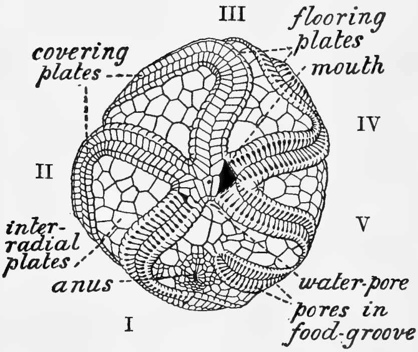


FIG. 3.

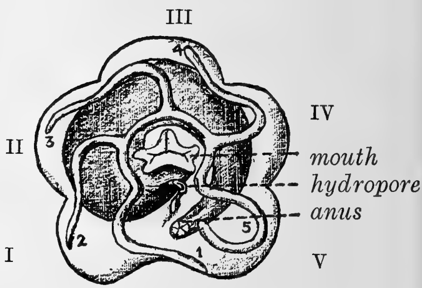


FIG. 4.

FIG. 1.—Diagram to illustrate MacBride and Gemmill's numbering of the rays in Asterias. The view is from the oral side. The position of the anus is that occupied by it in the adult, but it opens on the apical side.

FIG. 2.—Diagram of Asterias at the beginning of metamorphosis, based on the figures and description of Gemmill. The view is from the oral side, on which side the anus opens at this stage. The numbers I–V correspond with II, III, IV, V, I in Fig. 1. Hydrocoel pouches are numbered 1–5.

FIG. 3.—Oral face of *Edrioaster bigsbyi*. The numbers I–V correspond with those in Figs. 2 and 4, but not with those in Fig. 1.

FIG. 4.—Diagram to show the supposed relations of water-vascular system and gut in young Edrioaster. The view is from the oral side. The numbers I–V correspond with those in Fig. 2. The ends of the hydrocoel pouches 1, 2, 3, 4 enter rays 5, 1, 2, 3 respectively, and in this regard make those rays correspond with rays I, II, III, IV of Fig. 1. The hydropore leads into the stone-canal, and probably into a genital duct.

the attachment (e.g. Calceocrinidae) a strong secondary bilateralism has been superimposed on the pentamerism, and has generally quite obscured it. Pentamerism could never have arisen under such conditions.

Another objection to this imaginary ancestor springs from those sanitary principles that have proved so useful in elucidating the morphology of extinct Pelmatozoa (see especially "Caradocian Cystidea from Girvan", §§ 232, 583, 591; Trans. Roy. Soc. Edinburgh, vol. xlix, part 2, No. 6, 1913). The guiding idea is that the excreta should be removed as far as possible from the food intake and the respiratory organs, and at the same time in such a position that they will be carried away by currents. Now the imagined primitive Asterozoön contravenes those principles, because mouth, vent, and hydropore were certainly all on the oral face, and yet we are to suppose that face turned downwards towards the attachment.

Even if the ancestral Asterozoön, as imagined by Messrs. Gemmill and MacBride, could scarcely have been viable, it does not follow that the Pelmatozoic conception of the ancestor is any more in harmony with known facts and principles. Indeed, it is asserted that the facts of recent Asteroid embryology render it inadmissible. Let us consider some of these "very serious ontogenetic difficulties".

A reader who accepts the orientation of the rays adopted in Gemmill's paper on *Asterias rubens* (Phil. Trans., 1914), will speedily meet with stumbling-blocks.

In the larval stages of that form and of several others, the anus, the stalk, and the hydropore all lie between the horns of the hydrocoel crescent. The hydrocircus is formed by the closure of the horns in that interradius. It is therefore from this point that MacBride and Gemmill, very reasonably, start their numbering of the hydrocoel pouches. As the first pouch, they take that which lies towards the anterior end of the bilateral larva: if the embryo star be viewed with the mouth upwards, this is the pouch that forms the left horn of the crescent, so that the remaining numbers follow on in a solar direction. Those authors use the Roman numerals I–V, but, for a reason that will appear presently, it will conduce to clearness if for these particular structures we provisionally use the Arabic figures 1–5. The rays of the star with which these hydrocoel pouches eventually become associated are similarly numbered I–V by MacBride and Gemmill, i.e. ray I corresponds with pouch 1, II with 2, and so on. Thus, for the adult structure, Dr. Gemmill arrives at the annexed diagram (Fig. 1), which is copied from that in his memoir, but turned upside-down so as to render it more easily comparable with the arrangement in Pelmatozoa. Here the adult anus lies in interradius I/V, which marks the "Asterid plane" of Cuénot. It is not in this interradius but in the adjoining one (I/II, solar in oral, contrasolar in aboral aspect) that the madreporite and stone-canal of the adult are found. The latter interradius also corresponds with the brachiolarian notch, and bears a most important relation to the sagittal mesentery of the larva, and to the epigastric mesentery of the developing star.

In all the early Pelmatozoa, on the other hand, the hydropore, the anus, and presumably the closure of the hydrocoel are normally in a single interradius, which bears a definite relation to the branching of the rays, and therefore serves as the starting-point for their numbering.

Now since it is not immediately obvious how either of these sets of organs can have jumped over the intervening radius (I), this seems rather a fundamental difference. It is, I believe, capable of explanation on the Pelmatozoic theory; but before reverting to that let us consider some further facts of embryology.

First, note that in the recent adult starfish both anus and madreporite are on the apical surface. In the early stages, however, they are on the oral surface. Therefore they have migrated. Now while the madreporite remains between the same rays of the star as the original hydropore lay, the anus has changed. We are, however, unable to trace its migration because there is a gap due to closing of the larval intestine and the formation of a new rectum and proctodaeum. This fact alone should be enough to suggest that the evolution of the Asteroidea from the fixed Dipleurula cannot have been so simple and direct as claimed by Gemmill and MacBride and as represented in the latter's diagrams.

As regards the madreporite, the application of these facts to phylogeny is clear, because in the fossils we can trace the historical passage of the madreporite between the rays from an adoral, or oro-marginal, position to an adapical position (see Spencer, 1914, Mon. Brit. Pal. Ast.).

The anus is so obscure, if not absent, that its passage is less easily traced in those fossils. According to C. Schuchert,[1] "The only Paleozoic form in which an anal opening may exist visually is [the Ordovician] *Hudsonaster*. Here it is on the [adapical] disk between the central plate and the madreporite" (p. 13), apparently, then, still in the hydropore interradius; but the anal nature of the appearance is very doubtful (p. 39). In other fossil Echinoderms, however, the migration of the anus can be traced and is observed to follow the presumed line of the coiled gut. That is just what happens in the developing starfish: the coil of the gut shortens and the anus is consequently pulled in a contrasolar direction (as viewed from the oral pole), i.e. from the madreporite plane into the Asterid plane. Though the coil of the gut is thus obscured in Asteroidea, it is important to recognize that it really is of the same nature as in other Echinoderms (see *Treatise on Zoology*, 1900, p. 34).

Consequently, from the embryological and anatomical facts now placed in so clear a light by Dr. Gemmill, we can readily imagine how and why the anus, in its phylogenetic passage from the oral to the aboral surface, followed a course which was not straight but curved so as to bring it into the interradius where it now lies. Further we see that, whereas the anus was exposed to two forces or tendencies, of which its present position is the resultant, the madreporite was subject to only one, namely the tendency to pass

[1] "Revision of Paleozoic Stelleroidea," U.S. National Mus., Bull. 88, 20 March, 1915. This valuable work appeared some months after these paragraphs were first written.

from oral to apical along the straight plane of the stone-canal. Hence it did not change its interradius.

As was shown in "What is an Echinoderm?" these movements are precisely those which would naturally take place on the hypothesis of the origin of Asteroids from such a Pelmatozoön as *Edrioaster*. That hypothesis makes these movements very simple and inevitable, but the converse conclusion does not necessarily follow: the conclusion, namely, that because these movements must have taken place, therefore the ancestor of the Asteroids was an Edrioasteroid. All that is claimed is that the facts thus far are fully consistent with such a conclusion.

We turn now to the next difficulty: the position of the plane of closure of the hydrocoel. As already explained, this plane is placed by MacBride and Gemmill between their rays I and V, i.e. in the Asterid plane of Cuénot (my interradius IV/V).

In the primitive Pelmatozoön, so far as can be inferred from the embryology of *Antedon* and the anatomy of early forms, the closure of the hydrocoel was in what I have termed the M plane (see *Treatise on Zoology*, 1900, p. 20). This corresponds with MacBride and Gemmill's interradius I/II (my I/V).

It is important to notice here that in an Asteroid larva (*Bipinnaria asterigera*) described by Bury, the closure does still take place in the M plane (1895, Quart. Journ. Micr. Sci., vol. 38, p. 65).

Apart from the hydrocoel and its extensions, the food-grooves of Pelmatozoa (which are the initiators of the rays) are bilaterally symmetrical about the M plane. Therefore we are not surprised to find that in Asteroids this same plane is that in which the brachiolarian notch occurs and closes, and that the rudimentary rays (apart from the hydrocoel) are similarly bilaterally symmetrical about that plane (Fig. 2). Other relations of this plane have already been mentioned (see Gemmill, 1914, Phil. Trans., p. 277).

The M plane, therefore, is as fundamentally important a plane for Asteroidea as it is for Pelmatozoa. The Asterid plane is a plane of superimposed symmetry, due to the migration (*a*) of the anus, (*b*) of the hydrocoel-closure. One speaks of the "migration" of the hydrocoel-closure because it cannot be imagined that the closure takes place in a different part of the hydrocircus itself. If we postulate any homology whatever with Pelmatozoa, we can only explain the difference of position by supposing that the whole hydrocoel has shifted round. The extent of the shifting would be one-fifth of a circle, i.e. 72°; and the direction of the shifting, as viewed from the oral face, would be contrasolar. Such shifting need not involve the hydropore, with which the hydrocoel has only a secondary connection.

Now we know very well that, in those Asteroids where the hydrocoel-closure is in the Asterid plane, just such a shifting or torsion does take place in the early stages of metamorphosis. To quote Gemmill (1914, Phil. Trans., p. 251), "the disc undergoes torsion through about 75° in the (starfish) horizontal plane, counter-clockwise as viewed from the sucker." It must be remembered that the development of the lobes of the hydrocoel is quite independent

from that of the arms, and that only later on do the two sets become apposed or harmonized. The accounts given by the embryologists seem to prove that in certain Asteroids there actually is such a shifting of the whole hydrocoel that each lobe of it becomes applied, not to the ray to which it would (especially on any homology with Pelmatozoa) naturally belong, but to the neighbouring ray, just as though one were to twist a clock-face backwards, so that when the clock struck twelve the hands should point to twelve minutes past two (i.e. one-fifth of the clock-face).

This interpretation is confirmed by the exception; for in Bury's *Bipinnaria*, where the hydrocoel closes in the M plane, the fusion of the main hydrocoel lobes with the rays "is effected", says Bury, "without that rotation of the two series of organs noticed by Ludwig in Asterina" (1895, p. 68).

It seems legitimate to infer that in some remote ancestor of the Asteroids the closure of the hydrocoel took place in the M plane, and that the lobes 1 to 5 corresponded with the rays numbered I to V in the Pelmatozoa, but numbered respectively II, III, IV, V, I in the adult Asteroid by MacBride and Gemmill.

Why this torsion took place in some Asteroids we do not know. It may have been connected with the migration of the anus and the dragging of the mesenteries. That is a point which the embryologists do not as yet seem to have discussed.

It was, however, pointed out in "What is an Echinoderm?" that if any Asteroids were evolved from a pelmatozoön in which the food-grooves had a strong contrasolar curve (as in *Edrioaster bigsbyi*), then some such contrasolar torsion of the oral region through 72° would naturally accompany the straightening of the rays. Examination of Text-figures 3 and 4 will at once make this clear. This hypothesis works quite well so far as the hydrocoel is concerned, but seems to create a difficulty with regard to the hydropore, which, one might suppose, would also have been involved. We have to remember, however, that the hydropore and stone-canal did not necessarily accompany the hydrocoel, and when the madreporite had attained the aboral surface and escaped the influence of the rays, it might have been pulled back into its original interradius by the stone-canal.

Any exceptions, such as Bury's *Bipinnaria*, would, on this same hypothesis, be readily accounted for by supposing those starfish to derive from an Edrioasteroid like the Cambrian *Stromatocystis*, in which the rays have not acquired a curvature.

To consider the possible relations of the Pelmatozoa (Edrioasteroid or other) to the Echinoidea would unduly prolong the argument. Those to whom the present paper is intended to appeal agree with me that the Echinoidea no less than the Asteroidea must have had a fixed ancestor, and Professor MacBride, for one, would derive all Eleutherozoa from the Asteroid stem. If we can but agree as to the Asteroid ancestor, the rest follows.

The essential difference between us is that Messrs. MacBride and Gemmill believe the Asteroid to have evolved directly, mouth downwards, from the Dipleurula, whereas I would insert a true Pelmatozoic stage.

So far as the change in mode of life is concerned, their hypothesis is no easier than mine. Professor MacBride has made a number of ingenious suggestions, chiefly dependent on "the fundamental distinction which obtains at the present day between the habits of Eleutherozoa, which in the majority of cases are scavengers, devouring dead animals and organic detritus lying on the bottom, and those of Pelmatozoa, which to this day feed on Plankton captured by currents produced by the cilia covering their tentacles" (1914, *Embryology*, p. 564). Now that Dr. Gemmill has broken down the barrier of this "fundamental distinction" the hypotheses based on it lose much of their probability.

If we imagine an Edrioasteroid with loose attachment, liable to be overturned by currents, just as we know that individuals of *Stromatocystis* were overturned, then all we have to suppose is that some of the overturned individuals were able to survive the accident. This they would be able to do if they had fairly well-developed podia, such as are indicated by the anatomical evidence. Even without the overturning, the podia of such genera as *Edrioaster* and *Dinocystis* might have subserved locomotion; for in them the ends of the subvective grooves were brought into almost direct contact with the sea-floor. Indeed, it is hard to see how locomotion could have been avoided.

As for the alleged directness of individual development (which, as already pointed out, is not direct in some important particulars), this may well be more apparent than real. If it be direct, we are thrown back on 'idiosyncrasy' and 'hemiplegia' and misfits 'somehow displaced'. If, on the other hand, the stalk represents the last trace of a former pelmatozoic stage, we have to imagine that the greater part of that stage has been cut out. But what is more natural? In Ophiuroidea the fixed stage is omitted altogether. In Asteroidea it is not omitted but condensed. The later stage, in which the mouth is already directed downwards, has been pressed back so as to eliminate the supposed stage during which it passed upwards. The preservation of that stage in the ontogeny would have been a useless waste of energy.

Dr. Gemmill says that my view introduces "very serious ontogenetic difficulties". I am unable to see that the main ontogenetic difficulties are any better explained by the Gemmill–MacBride theory, which in its turn seems to me to introduce a fresh set of phylogenetic difficulties.

INDEX.

Page-references are preceded by an abbreviated form of the year of publication, thus . . . . '08, 549

When several page-numbers in succession fall within a single year, the year-reference is not repeated for each.

Text-figures are referred to by the number of the page on which they occur, with an additional subordinate number only where necessary, thus . . . . '99, 135 tf.

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The year of publication precedes the page-number on every sheet of the text, except sheet A, where volume-numbers were inserted. Of these V = '98, VI = '99, and VII = '00.

Names of species are indexed under the trivial name (in italics and never with an initial capital) followed by the generic name, thus . *levis*, *Edrioaster*.

The trivial names of species are also entered in an alphabetical list following the name of each genus with which they are associated (rightly or wrongly) in the text.

Stephen Austin and Sons, Ltd., Printers, Hertford.

A few copies of the following works are still to be had from the Author.

Index to Desor's Synopsis des Echinides Fossiles. 8vo. 48 pp. 1910. Price 9s. 0*d*.

"le complément indispensable du 'Synopsis' de Desor" Revue critique de Paléozoologie.

"Should prove of great use to every worker on Echinoids" Geological Magazine.

"Dr. Bather has supplied a long-felt want and has done a valuable service to all students of living and fossil echinoids" Nature.

Wachsmuth and Springer's Monograph on Crinoids. A Review reprinted in 64 pp. from the Geological Magazine for 1898–9, with Portrait, Obituary, and Bibliography of C. Wachsmuth, and an Index. Price 2*s*. 0*d*.

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"Observations très importantes . . . éclairées par des figures indispensables" Revue critique de Paléozoologie.

"His delightful Review" Ottawa Naturalist.